The association between temporal sensitivity, sense of agency, and occipital peak alpha frequency.

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General Abstract

For appropriate behaviour in response to one's surroundings, an accurate perception of the environment is essential. One key element of this is the grouping of temporal information. Temporal grouping is dependent on the individual`s temporal sensitivity and is reflected in the temporal binding window. Previous literature has shown alpha oscillations are a potential neural mechanism of temporal sensitivity. Moreover, there is preliminary evidence linking temporal sensitivity with time perception and sense of agency. However, the link between sense of agency and alpha oscillations has remained largely theoretical, with no studies directly investigating this link. Similarly, the link between time perception and alpha oscillations is not established, with the few studies that do directly assess this relationship allowing for alternative explanations. This thesis first reports three studies exploring the relationship between temporal binding window, time perception and sense of agency while also considered alpha oscillations as their potential neural mechanism. Findings indicated that the temporal binding window and sense of agency in simple action-outcome relationships are related processes, with alpha oscillations being a potential shared neural mechanism (Study 2). Yet, when complex action-outcome relationships are involved this link is less strong. That is, complex action-outcome relationships present a wider range of possible agency cues that are relied upon instead of temporal cues (Study3). When considering time perception, an association was not found with either temporal binding window or alpha oscillations (Study1). In the fourth study, we showed that both the sense of agency window and the temporal binding window could be modified by brief perceptual training, whereas alpha oscillations stayed unchanged. Taken together, these findings suggest that changes in cognitive processes take place immediately following the perceptual training due to temporarily shifting the point of subjective simultaneity towards the optimum in response to learning and development. However, for this change to become permanent, changes in neural

system (alpha oscillations) should be established. Such neural changes have shown to require three or more months of learning and development. While these findings primarily serve to show the existence of relationships between the above processes, they also provide substantial implications and suggestions for further research.

Overview of Chapters

Chapter 1: General Introduction

This chapter provides background information and key research relating to the association between temporal binding windows, time perception and sense of agency as well as their proposed neural mechanism – alpha oscillations. This chapter also discusses relevant research into the modification of the above processes. In particular, this discussion focuses on perceptual training and its observed effects.

Chapter 2: Individual differences in alpha frequency are associated with the time window of multisensory integration, but not time perception.

This chapter presents one experiment that aimed to explore to what degree, if any, time perception, the temporal binding window and alpha oscillations are related. As predicted a significant relationship between the temporal binding window and peak alpha frequency was observed. However, contradictory to the predictions, time perception was not linked with either of these. These findings are discussed with respect to the possible underlying mechanisms of multisensory integration and time perception.

Chapter 3: Temporal binding window and sense of agency are related processes modifiable via occipital tACS.

This chapter discusses one experiment that aimed to investigate the relationship between individual differences in the temporal binding window and individual differences in the sense of agency window. Furthermore, this study used occipital tACS at either 14Hz or 8Hz to attempt to modulate both of these processes. Although a direct relationship between the temporal binding window and the sense of agency window was not observed, we found that both of these were modified by tACS. More specifically, a narrower temporal binding window and sense of agency window was associated with 14Hz tACS stimulation and vice versa. Taken alongside other findings, these results suggest that the temporal binding window and the sense of agency window are related, and that they may share a common underlying neural mechanism (alpha peak frequency).

Chapter 4: The relationship between temporal sensitivity and sense of agency.

This chapter reports the findings of one experiment that aimed to further clarify the relationship between temporal sensitivity and sense of agency. In particular, this experiment explored this potential link in an agency task involving more complex action-outcome relationships. An association was found only during most distinctive manipulations (manipulations where a long lag was introduced to the movements of a cursor). What is more, this association was in contrast to the predictions. Namely, increased sensitivity of metacognition of agency was associated with a wider temporal binding window. This suggests that the relationship between the temporal binding window and sense of agency observed in previous studies is less prevalent when complex action-outcome relationships are involved, perhaps because a wider range of possible agency cues are present that are relied upon more than temporal cues.

Chapter 5: Perceptual training modifies temporal binding window and sense of agency but not alpha oscillations.

In this chapter, the final study of this thesis is discussed. This study explored the effects of perceptual training on the temporal binding window, sense of agency and the frequency of the alpha peak. Findings indicated that the sense of agency window and the temporal binding window were both reduced after perceptual training. These findings not only replicate the effects of perceptual training previously observed on temporal binding window but also presents novel findings indicating that perceptual training enhances the sense of agency when simple action-outcome relationships are involved. Moreover, these findings in combination with previous literature suggest that changes in cognitive processes take place immediately following the perceptual training but fade within a week. We propose that for this change to become permanent changes in neural system (alpha oscillations) should be established. Such neural changes have shown to require three or more months of learning and development. However, alpha oscillations stayed unchanged following perceptual training. We explain these findings in terms of characteristics of our study.

Chapter 6: General Discussion

This chapter draws together the findings of all four experiments and considers the implications. More specifically, it was argued that perhaps specifics of the tasks are mediating the association of time perception with temporal binding window and alpha oscillations. Regarding temporal binding window and alpha oscillations, a link was shown with alpha frequency but not alpha power, indicating that alpha frequency and alpha power are distinctive. In terms of the association between sense of agency and temporal binding window findings indicated that a link is present in simple action-outcome relationship but is less strong in complex action-outcome relationship. Lastly, the findings indicted that brief perceptual training temporarily modifies cognitive processes (sense of agency and temporal binding window). Furthermore, it was indicated and that for these changes to become permanent changes in neural processes (alpha oscillations) must become established. It was suggested that such changes can be induced via perceptual training of three or more months. Limitations and future directions are also discussed in this chapter.

Chapter One: General Introduction

Multisensory integration

In order to provide a context this section will begin with a brief and simplified overview of the sensory systems.

Senses

There are five basic senses: touch, sight, hearing, smell and taste. Each of these senses are perceived by a different sensory receptor which then send sensory information signals to the relevant part of the brain.

The somatic sensory system is responsible for perception of touch, such as pressure, temperature, light touch, vibration and pain (Coren et al., 1999). All tactile sensory information is received by the different neural receptors in the skin. These neural receptors are activated and signals travel along sensory nerves made up of bundled fibres that connect to neurons in the spinal cord. Then the ventral posterior nuclei relay information regarding touch and perception of bodily position to the primary somatosensory cortex in the cerebral cortex.

The visual sensory system is involved in the perception of sight with its sense organs being the eyes (Remington, 2011). Visual information enters via cornea and is then passed through the pupil and enters the lens which then focuses this information on retina where receptor cells are located. There are two types of receptor cells: rods and cones. Cones translate light into colours, central vision and details. The rods translate light into peripheral vision and motion. Information translated from the photons of light is sent as nerve impulses to the lateral geniculate nucleus and then Brodmann area 17. Here the nerve impulses are interpreted as images.

The auditory sensory system governs hearing with the sense organ being the ear (Musiek & Baran, 2018). Sound vibrations enter the ear and are funnelled into the external auditory canal that leads to the middle ear. There auditory ossicles (malleus, incus and stapes) vibrate. This leads to the oval window being pushed in and out and results in sending vibrations to the Organ of Corti in the inner ear. The Organ of Corti translates vibrations into electrochemical signals which are sent to vestibulocochlear nerve. From here the signals travel to ventral and dorsal cochlear nuclei and are sent via different paths to the medial geniculate nucleus and then relayed to the auditory cortex. Auditory cortex is located in the temporal lobe and has a role in the processing of auditory information.

The olfactory sensory system is responsible for sensing odours (Mori, 2014). Olfactory receptors are found in large numbers in the epithelium of the mucous membrane lining the upper part of the nasal cavity. The axons projecting from the olfactory receptor cells carry sensory information via the olfactory nerve to the olfactory bulb. Here the olfactory nerves end and the olfactory tract begins. The olfactory tract is band of nerve fibres that extend to the olfactory cortex in the temporal lobe of the brain. Here the olfactory sensory information is processed.

The gustatory sensory system is responsible for detecting five basic taste sensations (sweet, sour, salty, bitter, and savoury) with the tongue being the sense organ (Doty, 2015). The surface of the tongue contains taste buds which in turn contain the gustatory receptor cells. Once activated, gustatory receptors cells release neurotransmitters onto the dendrites of the facial, glossopharyngeal or vagus nerves. Axons from these cranial nerves then carry gustatory sensory information to the medulla from where the information is passed on to the ventral posterior nucleus. From there gustatory sensory information reaches the primary gustatory cortex where sensation of taste is processed.

Grouping of sensory information

Accurate integration of sensory information from different modalities is of paramount importance in order to perceive the world as whole and enable accurate and fast behavioural response (Welch & Warren, 1980). Often when something happens in the environment, this event generates sensory information in multiple domains. For instance, a falling tree generates both a crashing sound and the sight of the tree falling. However, due to different types of sensory information having different physical transmission times, each type of sensory information reaches the sensory receptors at a different time. Nevertheless, a unitary perception of the event is maintained. Hence, in order to effectively engage with the surroundings, it is fundamental that sensory information from events is accurately segregated and integrated. For nearly 3 decades, it has been argued that both spatial concurrence and temporal concurrence is key to grouping of sensory information (Mast et al., 2015; Spence, 2007; Stein & Meredith, 1993; Stein & Stanford, 2008). Spatial concurrence is when stimuli are presented in the same location. Whereas temporal concurrence is when the stimuli are presented at the same time. However, upon inspection of the literature it appears that spatial concurrence is vital for the grouping of sensory information only in specific cases (Spence, 2013). More specifically, spatial concurrence is necessary for grouping of sensory information if the space is relevant to the situation. Whereas, temporal concurrence is vital for grouping of sensory information irrespective of the specifics of the situation (Koelewijn et al., 2010; Van der Burg et al., 2008). It is argued (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017), that whether sensory information is bound together largely depends upon the perception of their temporal relationship (time difference of reaching sensory receptors). That is, sensory stimuli perceived further apart in time are less likely to be grouped than those perceived closer together. Hence this thesis will focus on temporal grouping of sensory information.

Temporal binding window

Multisensory perception is facilitated by the existence of a so-called ‘temporal binding window’ (TBW), the time frame within which temporal grouping of sensory information takes place (Colonius & Diederich, 2012; Dixon & Spitz, 1980; King, 2005; Lewkowicz & Ghazanfar, 2009; Spence & Squire, 2003; Van Wassenhove et al., 2007; Vatakis, 2013; Vroomen & Keetels, 2010). Given that each type of sensory information reaches the sensory receptors at a different time, the concept of TBW makes good ecological sense. An event occurring at a distance of 20 meters that produces visual sensory information and auditory sensory information can be taken as an illustrative example. The speed of light is 299 792 458 m/s whereas the speed of sound is 343 m/s. Hence, the visual sensory information arrives at the sense organ nearly instantaneously, whereas auditory sensory information arrives at the sense organ around 60ms later. Considering the discrepancy between the arrival times of sensory information from different modalities by the same event, a TBW enables the integration of such sensory information and consequently facilitates perception of the event. Previous studies exploring temporal constraints of multisensory integration demonstrated that sensory information that is separated by up to 350ms can be perceived as simultaneous and thus coming from the same event (Zmigrod & Hommel, 2011). The width of the TBW varies depending on the specifics of the situation such as, the duration and intensity of the sensory information (Boenke et al., 2009), the type of the sensory information being combined (Fujisaki & Nishida, 2009), and the complexity of the sensory information (Stevenson & Wallace, 2013; Van Eijk et al., 2008; Van Wassenhove et al., 2007). Moreover, the width of the TBW also differs between individuals (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). Such differences between individuals are due to the difference in an individual`s temporal sensitivity (the ability to detect time-based discrepancy between two stimuli, which regulates grouping of sensory information) (Colonius & Diederich, 2004). Visual and auditory modalities are by far the most frequently investigated sensory modalities and as such methodology to assess the TBW of audio-visual sensory information has been robustly established. Given that the extensive research in the area of audio-visual sensory information have led to established methodology and TBW can be assessed using any two sensory modalities this thesis will assess TBW by focusing on audio-visual sensory information integration.

Methodology of measuring temporal binding window

In order to assess TBW, illusionary tasks, whose perception relies on the multisensory integration, have been employed. Such illusionary tasks provide indications of the width of the TBW. More specifically, proneness to integrate multisensory information is argued to indirectly correspond to the width of the TBW, as when the width of the TBW is wide, multisensory information is integrated on more occasions than when the width of the TBW is narrow. Introducing a range of temporal disparities between the stimuli allows one to assess the width of the TBW directly. That is, the temporal disparity between stimuli at which a participant no longer integrates stimuli is taken as the width of their TBW. Due to the prominence of the grouping of sensory information, a vast number of studies have explored these factors in the context of TBW. In turn giving rise to several experimental paradigms (Sarko et al., 2012).

One indirect measure of the width of the TBW uses the McGurk effect illusion (McGurk & MacDonald, 1976; Pearl et al., 2009; White et al., 2014). This illusion consists of a participant observing a model saying compatible but mismatched syllables of the simultaneous auditory syllables (i.e. auditory stimulus of ga ga, visual stimulus of da da). Although the auditory stimulus and visual stimulus are well recognized alone, when presented simultaneously, they give rise to an illusion that is often heard as a combination of both stimuli (i.e. ba ba). It shows that auditory and visual information are integrated into a unified percept. As previously mentioned, temporal disparity between the stimuli is necessary to determine the width of the TBW. Given that McGurk effect illusion lacks such disparity as both stimuli are presented simultaneously, conclusions only regarding the proneness to integrate multisensory information can be made. When the width of the TBW is wide multisensory information is integrated on more occasions than when the width of the TBW is narrow. Hence, those with wider TBW are expected to be more susceptible to the McGurk effect illusion than those with narrower TBW. As such the McGurk effect illusion provides an indirect measure of the width of the TBW.

One commonly used experimental paradigm that directly assesses the width of the TBW is a simultaneity judgment task (Engel & Dougherty, 1971; Fenner et al., 2020; Stevenson et al., 2010; Zampini et al., 2005). In this task visual and auditory stimuli are delivered simultaneously or non-simultaneously with either visual or auditory stimuli leading at various Stimulus Onset Asynchronies (SOAs). SOA denotes the amount of time between the start of one stimulus and the start of another stimulus. Participants are instructed to report whether the auditory and visual stimuli were presented at the same time or different time. Responses reporting simultaneity are then plotted as a function of SOAs in percentages. Data is then fitted to a psychometric function and its inflection point (a point on the curve in which the concavity changes) corresponding to 50% simultaneity judgements is taken as the width of the TBW. A similar experimental paradigm is that of temporal order judgement task (Basharat et al., 2018; Hendrich et al., 2012). Like in the simultaneity judgment task, visual and auditory stimuli are presented with either one of the modalities leading at various SOAs. However, this task does not include simultaneous presentation of the visual and auditory stimuli. Hence, this task requires one to judge which modality is presented first. Here responses are also plotted as a function of SOAs in percentages and fitted to a psychometric function. Similarly, the inflection point corresponding to 50% of judgements in favour of one of the modalities is taken as the width of the TBW.

Recent reviews of the literature on this topic (Hirst et al., 2020; Keil, 2020) have shown that the double-flash illusion is the most frequently used experimental paradigm to directly explore the TBW. This task involves simultaneous presentation of visual and auditory stimuli followed by a presentation of a second auditory stimulus after various time delays. If the second auditory stimulus occurs within the individual's TBW not just the first auditory stimulus is integrated with the visual stimulus but also the second auditory stimulus. This creates an illusion whereby participants report experiencing two flashes despite only one flash being presented. The delay at which an individual no longer perceive two flashes is taken as the width of their TBW. The results robustly show that as the delay increases the multisensory integration decreases, and the illusion disappears. As in the previous experimental paradigms described above, responses are plotted as a function of SOAs in percentages. Similarly, a psychometric function is then fitted to obtained values returning an inflection point representing the point of decay of the illusion (point corresponding to 50% of judgements in favour of one flash). This inflection point is taken as an index of the TBW.

The reasoning behind the favouring of the double-flash illusion experimental paradigm seems to be the implicit manner in which this experimental paradigm allows measurement of the width of the TBW, thus leading to reliable and confound free results. That is, simultaneity judgement tasks and temporal order judgement tasks involve participants making conscious decision regarding the simultaneity or order of the stimuli. Hence, it is likely that during the judgement, not only the implicit process of integrating multisensory information is involved, but also the more explicit process of time perception is involved. More specifically, in these experimental paradigms, an implicit process of integrating multisensory information occurs due to the stimuli (flash and beep) being integrated within the TBW. More explicit processing of the temporal structure also occurs as participants are directly instructed to determine whether or not a flash and beep occur at the same time; resulting in participants consciously thinking about time between the stimuli. In contrast, in the double-flash illusion task, only the implicit process of integration of multisensory information seems to occur. Specifically, here participants must rely on this process solely as they are asked to only concentrate on the number of flashes perceived and hence no conscious thinking about time is involved. Given the above it seems that the most reliable experimental paradigm to measure the width of the TBW is double-flash illusion task. Hence, this thesis will employ this methodology.

Neural mechanism of grouping of temporal information

Electroencephalography

Electroencephalography (EEG) is a non-invasive method to directly record the electrical activity of the brain from the surface of the scalp via metal electrodes and conductive gel and was first used by neurologist Hans Berger in the 1920s (Jung & Berger, 1979). Given that electrical activity that reaches scalp from cognitive processes is fairly weak the recorded data is digitized and sent to an amplifier. EEG also has very high time resolution and can pick up very weak electrical activity which is necessary to capture cognitive processes in real time (Cohen, 2011).

The human brain contains billions of neurons with each neuron forming connections with thousands of other neurons. Neural activity is observable as oscillations in scalp-recorded EEG, and are often informally known as ‘brainwaves’. Different states of consciousness give rise to different neural connections and thus the resulting oscillations are thought to be related to the state of consciousness (Calomeni et al., 2017). Different types of oscillations are recognised based on the pattern of amplitudes and frequencies. There are five dominant oscillations: gamma, beta, alpha, theta and delta. Gamma oscillations (Jensen et al., 2007) have frequency above 30Hz and are the fastest oscillations detectable. Amongst other things, these oscillations are associated with heightened perception, learning and problem-solving and as such are involved in simultaneous processing of information from different parts of the brain. Beta oscillations (Schmidt et al., 2019) are between 13Hz and 32Hz present during active thinking. For example, when engaging in active conversation, decision making, problem solving or active learning. Alpha oscillations (Zhou et al., 2021) range from 7Hz to 14Hz and are associated with the awake state during physical and mental relaxation and thought to play an important role in setting the brain's internal state. Theta oscillations (Baijal & Srinivasan, 2010) are between 4Hz and 8Hz. These oscillations are associated with deep relaxation, reduced consciousness and creativity. Delta oscillations (Langille, 2019) are the slowest oscillations detectable ranging from 0.5Hz to 4Hz. These oscillations are strongly associated with sleep and dreaming. One strong candidate for being a neural mechanism of the temporal grouping of sensory information seem to be alpha oscillations (Cecere et al., 2015; Hirst et al., 2020; Keil, 2020; Keil & Senkowski, 2017; Migliorati et al., 2020), thus these oscillations will be the focus of the thesis.

Alpha oscillations and temporal binding window

It has been suggested that a higher (faster) alpha frequency provides a narrower excitatory phase and thus results in a higher temporal sensitivity, allowing detection of a shorter temporal discrepancy between two stimuli (Van Rullen, 2016). More specifically, higher alpha frequency leads to narrower oscillatory cycle. In turn, stimuli that fall into the same oscillatory cycle are bound into a single percept, while two stimuli falling into separate cycles are separated into two distinct temporal events. Given this, the temporal sensitivity and consequently the detection of temporal discrepancies increases along with an increase in alpha frequency. As numerous studies have shown, higher temporal sensitivity gives rise to shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews), this suggests a link between alpha peak frequency and the TBW. As previously discussed, TBW is the time frame within which the grouping of sensory information takes place (Colonius & Diederich, 2004). In turn, such grouping of sensory information is dependent on the temporal sensitivity, the ability to detect a time-based discrepancy between two stimuli. Thus, it is rational that higher temporal sensitivity would give rise to shorter width of the TBW. Further support is provided by studies directly investigating relationship between alpha peak frequency and TBW.

Correlational studies examining TBW and alpha oscillations include those conducted by Cecere et al. (2015) and Keil and Senkowski (2017). Cecere et al. (2015) used double-flash illusion, as described earlier, to assess the width of the TBW. In addition to measuring TBW, alpha oscillations were also measured via EEG during the double-flash illusion. The results showed that individual differences in the alpha cycle correlated positively with the inflection point. Similarly, Keil and Senkowski (2017) employed high-density EEG-study and found individuals with a lower alpha frequency showed higher susceptibility to the double-flash illusions. Both studies indicate that as individual alpha frequency increases, the width of the TBW decreases. In addition, a recent study conducted by Migliorati et al. (2020) showed that individual alpha frequency is not just associated with the width of the TBW when audio-visual integration is concerned but also in case of visuo-tactile integration. More specifically, Migliorati et al. (2020) used a visuo-tactile simultaneity judgment task to assess the width of the TBW. The task involved a participant holding a black foam cube. The tactile stimulus was delivered on the index finger via constant current electrical stimulator. The visual stimulus in the form of a white circle was displayed on the foam cube close to the tip of index finger. Either a visual or a tactile stimulus was presented followed, after a variable delay, by the stimulus in the other sensory modality. Individual alpha frequency was recorded during the visuo-tactile simultaneity judgment task using EEG. It was found that faster individual alpha frequency was associated with a narrower TBW.

Furthermore, there has also been causal evidence to support the link between individual alpha frequency and TBW. In addition to recording individual alpha frequency via EEG, Cecere et al. (2015) used neuromodulation to alter the individual alpha frequency. More specifically, transcranial alternating current stimulation (tACS) was used at either each participant's individual alpha frequency or individual alpha frequency +/-2Hz. Hence, participants received continuous tACS at one of three possible frequencies throughout the double-flash illusion task. Findings indicated that neuromodulation (via tACS) of the individual alpha frequency alters the width of the TBW accordingly (increased frequency of the alpha peak was associated with decreased width of the TBW). Despite the existing literature providing a clear link between alpha peak frequency and the TBW, it lacks replications of causal evidence. Thus, this thesis will incorporate a constructive replication of Cecere et al. (2015) methodology in order to further validate the relationship between alpha peak frequency and the TBW.

Link between time perception, alpha oscillations and temporal binding window

Time perception

Time perception is a fundamental element for awareness of the environment. Not just the present but also the past and the future as it connects memories with the current state and expectations. One of the most prominent and accepted frameworks of time perception (Church, 1984; Treisman et al., 1990) seems to be that of Scalar Expectancy Theory (Gibbon et al., 1984). The rationale behind this theory is the internal clock model (Treisman, 1963) within which the main components are the pacemaker and the accumulator. It is theorised that the pacemaker sets pulses of various rates that are sent to the accumulator and determines the units that the accumulator stores. Higher pulse rates will lead to more pulses being sent to the accumulator and thus store more units in the accumulator. In turn this is argued to result in an overestimation of the subjective perception of time and vice versa.

Pulses in the pacemaker in the Scalar Expectancy Theory have been proposed to be determined by arousal (Wittmann & Van Wassenhove, 2009; Wittmann et al., 2010). That is, high arousal leads to an increase in the pulse frequency of the pacemaker resulting in overestimation of time (Gil & Droit-Volet, 2012; Grecucci et al., 2014; Ogden et al., 2015; Yoo & Lee, 2015; Mioni et al., 2016). For example, Gil and Droit-Volet (2012) demonstrated this by evoking arousal via images from the International Affective Picture System (Bradley & Lang, 1994; Lang et al., 1997). To stimulate high arousal, pictures of disgust and sadness were presented, to stimulate low arousal, pictures of fear were presented and for the control condition, neutral images were presented. Participants were presented with the pictures with various presentations (200ms to 1600ms) and were required to estimate the duration of the picture presentation. It was found that high arousal led to overestimation of time.

In terms of the neural basis of the pulse frequency of the pacemaker, it seems that alpha oscillations are a strong candidate. Namely, high arousal has been linked to alpha oscillations (Luft & Bhattacharya, 2015). Luft and Bhattacharya (2015) investigated the relationship between arousal, heartbeat evoked potential and alpha oscillations. Findings indicated that higher arousal was associated with a higher heartbeat evoked potential and lower alpha frequency. This seems to be in line with Treisman (1963; 2013) postulating that the pulses of the pacemaker are driven by the alpha oscillations. In particular, it can be reasoned that as the arousal determines the pulses of the pacemaker (Wittmann & Van Wassenhove, 2009; Wittmann et al., 2010) and arousal is negatively correlated with alpha oscillations (Luft & Bhattacharya, 2015) it is plausible that alpha oscillations are the neural basis of the pulse frequency of the pacemaker.

When considering pulses stored in the accumulator, the Attentional Gate Model (Zakay & Block, 1996) suggests that attention influences the amount of pulses that are sent from the pacemaker to the accumulator (Droit-Volet & Meck, 2007; Ogden et al., 2015; Wearden & Penton-Voak, 1995; Wearden et al., 2010). The pacemaker begins to send pulses to the accumulator once the interval needing to be timed is recognised, with this process concluding once the timed interval has ceased. When attention is allocated to timing, more pulses can be sent from the pacemaker to the accumulator. In other words, when attention is allocated to timing a prompt detection of beginning and end of timed interval is ensured, promoting accuracy of time perception. However, when attention is diverted elsewhere, the detection of the beginning and end of timed interval is compromised, leading to underestimation or overestimation of the time interval.

Methodology of measuring time perception

Throughout the existing literature various methods have been used to explore time perception. The filled duration illusion is considered to be one of the most robust, well supported and widely used method to assess time perception (Thomas & Brown, 1974; Wearden et al., 2007; Williams et al., 2019). This illusion refers to the fact that participants experience a filled interval to be longer than an empty interval (Plourde et al., 2008). In addition, it has been shown that judgements regarding filled intervals have less variability than judgements regarding empty intervals (Rammsayer & Lima, 1991; Wearden et al., 2007). There are many variations of the filled duration illusion found in literature. For example, a filled interval can be filled by a continuous stimulus or regularly spaced stimuli, an empty interval can have a short stimulus presented at the beginning and end of the interval or consist of irregularly spaced stimuli, and any sensory modality can be used to present the stimuli. Not surprisingly, the strength of the effect of the illusion varies between the different versions (Buffardi, 1971; Foley et al., 2004; Horr & Di Luca, 2015; Schiffman & Bobko, 1977). It seems that the most established version with strongest effect of the illusion involves a filled interval that consists of a single tone presented for the duration of the target interval, and an empty interval that encompasses two short tones presented at the beginning and end of the target interval. Participants are asked to estimate the duration of the tone, or the gap between tones and are provided a possible range. The effect of the illusion is determined by first calculating the slope (the increase in perceived time as a function of actual time) for the filled and empty intervals, and then calculating the difference in this slope. Previous research (Fenner et al., 2020; see next section for further details) has shown that individual differences in this illusion are associated with variation in the TBW, making it an ideal paradigm to use in the current research.

Time perception and temporal binding window

Existing literature contains some evidence linking TBW with time perception. More specifically, there is evidence suggesting that individual differences in temporal sensitivity are linked with individual differences in time perception. Fenner et al. (2020) measured the width of the TBW, using a simultaneity judgement task (described previously), and time perception, using the filled duration illusion (described previously). They found a positive correlation between the width of the TBW and the magnitude of the effect of the filled duration illusion.

Further support for a link between time perception and the TBW is provided by developmental studies. These studies showed that children have a larger filled duration illusion effect and a wider TBW than adults, suggesting that individual differences in time perception are linked with individual differences in TBW. In terms of time perception, Droit-Volet (2008) investigated time perception in children compared to adults by using filled duration illusion. In this version of filled duration illusion participants familiarised themselves with standard long and standard short durations. Thereafter, participants were provided with filled and empty intervals at various durations and had to judge whether the interval correspond to the short standard or the long standard. Results revealed that the effect of the filled duration illusion was larger in children than adults. Regarding TBW, Wang et al. (2005) investigated the width of TBW in children and young adults. An auditory oddball paradigm was used to assess the width of the TBW. This paradigm involves presentation of a frequency deviant immediately followed by an intensity deviant amongst standard frequencies and intensities. Thereafter, with various delay (50ms, 200ms, 250ms and 300ms), a second frequency deviant followed by intensity deviant is presented. If both deviants are within the person's TBW, integration occurs. However, if second deviant is not within the person`s TBW, such integration does not take place. Mismatch negativity, a component of event-related brain potentials used as a neurophysiological index of acoustic change, was recorded via EEG and used to determine the width of the TBW. That is, if only one mismatch negativity component is elicited integration has taken place, whereas two mismatch negativity components are elicited segregation has taken place. Thus, the delay at which only one mismatch negativity component is elicited is used as an index of the width of the TBW. Findings suggested that children have wider TBW compared to young adults. As can be seen, very limited evidence exists regarding the link between TBW and time perception with only one study to date directly investigating individual differences in TBW and time perception. Thus, this thesis will examine this association in order to accumulate evidence and advance understanding of the so far observed relationship.

Time perception and alpha oscillations

If it is the case that individual differences in TBW are linked with individual differences in time perception, it is plausible that these two processes also have a common underlying neural mechanism. Higher alpha frequency leads to higher temporal sensitivity, and higher temporal sensitivity gives rise to shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews). In addition, existing literature contains correlational evidence (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020) as well as causal evidence (Cecere et al., 2015) in support of the notion that the frequency of alpha peak is likely to be neural mechanism of TBW. The conceptualization behind alpha oscillations being the neural mechanism of time perception is provided by Scalar Expectancy Theory (Gibbon et al., 1984) and the proposed embedded internal clock model (Treisman, 1963) as previously discussed. Additionally, studies within the existing literature, at least partially, support the link between alpha oscillations and time perception (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020).

For example, Horr et al. (2016) used the filled duration illusion to investigate time perception and neural mechanisms. Participants were presented with two intervals per trial ranging from 500ms to 1500ms and had to decide which of the two was longer in duration. One type of interval was filled with regularly spaced tones and other with irregularly spaced tones. EEG was used to record frequency of the alpha peak. Findings indicated that alpha frequency was associated with time perception. However, it is impossible to exclude whether or not the task used triggered neural entrainment that can drive distortions in time perception (Matthews et al., 2014), and that these in turn might be mediated by alpha oscillations. Neural entrainment refers to the synchronization of neural activity with the periodic properties of external stimuli (Obleser & Kayser, 2019). That is, entrained oscillations arise from the realignment of the phase of ongoing oscillations to the driving stimulus. Given that both intervals in the Horr et al. (2016) study were filled with either regularly or irregularly spaced tones it is likely that this led to entrained alpha oscillations. As alpha oscillations are argued to potentially be neural basis of the pulse frequency of the pacemaker and the pulse frequency of the pacemaker are argued to drive subjective estimation of time (Gibbon et al., 1984) it is not possible to exclude the possibility that stimuli in the Horr et al. (2016) study did not confound time perception.

Glicksohn et al. (2009) provide another example where support for a relationship between the frequency of alpha peak and time perception was found. Their study involved participants having to produce target intervals of 4, 8, 16 and 32s. EEG was used to record frequency of alpha peak. It was found that increased alpha peak frequency leads to production of longer intervals. However, uncertainty regarding the results in this study arises from the durations of the time intervals used. In particular, the time intervals used raised the possibility that participants used chronometric counting. Hence it could be argued that the relationship between the alpha peak frequency and time perception is being mediated by the chronometric counting (Bizo et al., 2006) in Glicksohn et al. (2009) study.

Another study that at least partially supports the relationship between the frequency of alpha peak and time perception was conducted by Mioni et al. (2020). In this study participants were required to learn a reference interval (600ms). Thereafter, participants were required to judge comparison intervals of various sizes (300ms to 900ms in 100ms steps) in terms of their comparison to the reference interval. Throughout the behavioural task participants were subjected to continuous tACS stimulation at either their alpha peak frequency or at individual alpha peak frequency -/+2Hz. Results indicated that increased alpha peak frequency leads to intervals being perceived as longer. This led to the proposal that alpha peak frequency could be the neural basis of time perception. However, participants learned the reference interval without tACS stimulation while comparison intervals were presented during tACS stimulation. Given that tACS stimulation is generating a small shift in point of subjective equality and comparison intervals are set in 100ms steps (approximate alpha range; see Cecere et al. 2015) it is to be expected that tACS stimulation will result in observed findings. Hence, it is not clear whether this task is measuring time perception or temporal sensitivity.

Despite there being preliminary support in terms of alpha peak frequency being the neural mechanism of time perception, robust conclusions cannot be made. Given that existing studies on the topic have methodological limitations this thesis will be attempting to eliminate these shortcomings while exploring relationship between alpha peak frequency and time perception.

Link between sense of agency, alpha oscillations and temporal binding window

Sense of agency

Sense of agency (SoA) refers to the feeling of being in control of one's actions and their associated outcomes (i.e. the feeling of having caused a sensory event in the environment) (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). Most actions and outcomes contain some delay. Even simple action-outcome event such as pressing a switch to turn on the light involves certain delays. Despite such delays, SoA is experienced. If the action and its sensory outcome occur within a specific temporal interval, during which the action and the outcome is integrated, one experiences agency for the action and the outcome. This window, defined as a temporal interval within which SoA is experienced, has been referred to as the time window of SoA (Farrer et al., 2013). If the outcome is deferred beyond such temporal interval, the action and the outcome is segregated, hence agency is no longer experienced. As such, temporal cues seem to play an important part in generating our sense of agency.

However, SoA is influenced not only by temporal cues (Chambon et al., 2014; Moore & Fletcher, 2012). It is known that SoA is modulated by different cues in addition to the temporal relationship between action and outcome (Chambon et al., 2014; Moore & Fletcher, 2012). For example, SoA can also be influenced by action selection fluency (Chambon et al., 2014; Wenke et al., 2010). That is the notion that SoA is influenced by the choice of action before the action itself occurs (Chambon & Haggard, 2012). For instance, some traffic light buttons are ineffective. However, when pressing the traffic light button and the light changes individuals feel that the action of pressing the traffic light button has been caused by them McRaney (2013). SoA can also be influenced by the consistency between a predicted and actual outcome. Here SoA can be explained both in terms of predictive processes (Frith et al., 2000), and in terms of postdictive confabulation (Wegner, 2002). This might also include integrating prior information to inform SoA (Moore & Fletcher, 2012). Prior information may include possible alternative causes of the observed action outcome or whether the action was freely selected or not. Furthermore, in addition to being dependant on different cues, SoA also varies under different contexts, and between individuals (Sidarus et al., 2017).

Although SoA is informed by multiply cues, SoA is not always an accurate representation of the reality. For example, many traffic light buttons are ineffective in this context as the changing of the traffic lights is linked to a timer. Hence, depending on the timer, the pressing of a traffic light button and the traffic lights changing can involve a delay. Despite this, McRaney (2013) showed that most individuals experienced SoA over a change of traffic lights after pressing the traffic light button.

Methodology of measuring sense of agency

Existing literature contains numerous theories of SoA with the most prominent being cue integration theory (Moore & Fletcher, 2012; Pacherie, 2013; Synofzik et al., 2008; Vosgerau & Synofzik, 2012). This theory states that SoA is divided into a feeling of agency and a judgment of agency. Feeling of agency involves feeling of being the agent of an action and thus refers to low-level processing. Whereas judgment of agency involves judgment of being an agent of an action and thus refer to high-level processing. Given the different levels of cognitive processing involved these two aspects are assessed differently. Namely, the former is assessed using implicit measures while latter is assessed using explicit measures (Haggard, 2017).

In terms of implicit measures, intentional binding is the most widely used method (Haggard & Tsakiris, 2009). Intentional binding refers to the compression of the subjective perception of time interval between an action and outcome. The two most frequently used methods to measure intentional binding are a clock reading paradigm (Libet et al., 1983) and an interval estimation paradigm (Engbert et al., 2007). In the former, participants report the clock-hand position at the time when they pressed the key or heard a tone following the keypress (Haggard et al., 2002). These 'operant' conditions are then compared to 'baseline' trials where participants report the timing of a tone in the absence of an action, or an action in the absence of a tone. In the interval estimation paradigm, participants are asked to estimate the temporal interval between an action and its outcome (Engbert et al., 2007). When considering explicit measures, predominately binary judgments and Likert-scale ratings have been used. Methodology involving binary judgment is used in the tasks that require judgements in terms of whether or not the outcome is caused by the participants; for instance, judging whether a cursor movement on a monitor is the outcome of one`s action or someone else`s action (Franck et al., 2001). Whereas, Likert-scale ratings are used in the tasks that require participants to rate their degree of agreement with a statement such as "I caused the outcome" (Sato & Yasuda, 2005). Given that this thesis is concerned with the judgment of agency, an explicit measure of SoA will be employed.

Sense of agency and temporal binding window

Temporal grouping of sensory information is dependent on temporal sensitivity - the ability to detect a time-based discrepancy between two stimuli (Colonius & Diederich, 2004). The time frame within which temporal grouping of sensory information takes place is known as the TBW. There is also evidence suggesting that temporal grouping of sensory information plays a pivotal role in SoA (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989).

Previous studies have shown that increasing the interval between an action and an associated sensory outcome leads to a reduction in SoA (Shanks et al., 1989). Shanks et al. (1989) conducted 3 experiments all of which involved performing an action (pressing a key on a keyboard) that triggered an outcome on the computer screen with various delays. Participants were required to judge the extent to which the action caused the outcome. Findings across experiments showed that increasing the delay reduced the judgements of causality.

In addition, SoA seems to depend on temporal grouping of actions and outcomes. Kawabe et al. (2013) conducted an experiment where participants pressed a key on the keyboard (action) that triggered the appearance of a dark square (outcome) with various delays introduced. In one condition, a white flash appeared on the screen immediately after the key press (action), whereas in the other condition there was no flash. Participants were required to judge whether the key press (action) triggered the dark square (outcome) to appear on the screen. Results showed significantly weaker SoA during the white flash condition compared to the no white flash condition. This finding was taken to indicate that SoA for an outcome can be reduced by the presence of an additional sensory event coinciding with the action because this event, rather than the outcome, is integrated with the action. As such, this suggests that temporal grouping of sensory events can influence the experience of agency.

Farrer et al. (2013) proposed that if action and outcome occur within a specific temporal interval, within which the action and the outcome are integrated, one experiences a greater SoA. This was shown in their study, where participants were required to perform an action (a button press) that elicited an outcome (appearance of a circle on a screen) with various delays and to report their SoA over that outcome. Findings indicated that participants were more likely to report SoA for the outcome at shorter delays as opposed to longer delays, supporting the notion that SoA depends on the temporal relationship between action and outcome.

Given that temporal grouping of sensory information is an important determinant of SoA, it is plausible that individual differences in TBW are associated with the individual differences in the SoA window. However, existing literature lacks studies exploring this association directly, with only one previous study (Venskus et al., 2021 - experiment 1 and 2)[1] undertaking such an investigation. More specifically, TBW was shown to positively correlate with SoA (Venskus et al., 2021 - experiment 1 and 2). Thus, this thesis aims to build on this finding and explore the degree to which, if any, individual differences in the TBW correlate with individual differences in the SoA.

Sense of agency and alpha oscillations

If temporal grouping of sensory information links the TBW and SoA, it is plausible that these two processes also have a common underlying neural mechanism. As previously discussed, alpha oscillations have been shown to be neural mechanism of TBW (Gibbon et al., 1984; Glicksohn et al., 2009; Horr et al., 2016; Luft & Bhattacharya, 2015; Mioni et al., 2020; Treisman, 1963; Treisman, 2013; Wittmann & Van Wassenhove, 2009; Wittmann et al., 2010). Higher alpha frequency leads to higher temporal sensitivity, and higher temporal sensitivity gives rise to shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews). In addition, existing literature contains correlational evidence (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020) as well as causal evidence (Cecere et al.,

[1] *In Venskus et al. (2021) the first 2 experiments were conducted by collaborators in Italy, and do not form part of this thesis. Experiment 3 followed up on that work, and was eventually combined to form a manuscript. Therefore, only experiment 3 is described in this thesis, with experiments 1 and 2 forming part of the existing literature.*

2015) in support of the notion that the frequency of alpha peak is likely to be the neural mechanism of TBW. Thus, it is plausible that alpha oscillations may underlie the contribution of temporal grouping to SoA.

Evidence supporting the notion that alpha oscillations underlie the contribution of temporal grouping to SoA are somewhat indirect. As previously discussed, recent evidence has shown that time perception is linked to the TBW (Fenner et al., 2020), and alpha oscillations (Horr et al., 2016; Glicksohn et al., 2009) as well as can be modulated by tACS in the alpha frequency range (Mioni et al., 2020). In particular, Fenner et al. (2020) found a positive correlation between the width of the TBW and the magnitude of the effect of the filled duration illusion. Horr et al. (2016) findings indicated that alpha power has been linked to time perception. Whereas, Glicksohn et al. (2009) provide support for relationship between the frequency of alpha peak and time perception. The Mioni et al. (2020) findings indicated that increased frequency of alpha peak leads to intervals being perceived as longer. As highlighted above, SoA is highly dependent on the interval between action and outcome (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). As such, if SoA depends in part on the time interval between action and outcome, and on the perception of this interval, then it follows that SoA might relate to alpha peak frequency. To date, the existing literature lacks studies exploring the link between SoA and alpha peak frequency. This thesis will explore such relationship by examining whether occipital tACS stimulation alters the width of the SoA window as well as the TBW.

Neuroplasticity – temporal binding window, alpha oscillations, sense of agency and time perception

Neuroplasticity

About 130 years ago, William James introduced the idea of neuroplasticity (James, 1890). However, only in 1948 was the term ‘neuroplasticity’ was first defined (Konorski, 1948). ‘Neuro’ refers to neurons found within the brain while ‘plasticity’ refers to the brain's ability to change and adapt as a result of experience. Neuroplasticity advocates the stance that the brain is able reorganize pathways, create new connections and even create new neurons (Doidge, 2007). In other words, the neural system is able to modify in order to adapt to changes in the environment/sensory input. Neuroplasticity is often divided into 2 types: functional neuroplasticity and structural neuroplasticity.

Functional neuroplasticity (Grafman, 2000) refers to the brain's ability to move functions from a damaged area of the brain to other undamaged areas. Existing inactive neural pathways or neural pathways already in use begin to carry out lost functions. At the beginning this process is fast but soon slows down. Therapeutic rehabilitation can accelerate functional neuroplasticity via multiple rehabilitation programmes. Functional neuroplasticity includes processes such as axonal sprouting, homologous area adaptation, cross-modal reassignment, map expansion and compensatory masquerade. Axonal sprouting refers to intact axons growing new nerve endings which then connects to impaired neurons to re-establish the damaged neural pathway. Intact axons can also make connections to other intact neurons to establish a new neural pathway that can undertake the function of a damaged pathway. Homologous area adaptation involves function of the damaged part of the brain being taken over by the same part but in the opposite hemisphere. However, such shifting displaces some of the functions already there, thus leading both functions to lose optimum performance (Grafman, 2000). Cross-modal reassignment refers to use of brain area denoted to one sensory modality to be used for processing another sensory modality. For example, people that have become blind no longer receive visual sensory modality, thus the brain area devoted to that sensory modality is unused. As this brain area is unused another sensory modality can take over. One example is where blind individuals use visual cortex to process auditory modality (Thaler et al., 2010). Map expansion is when a brain area used extensively expands to accommodate such usage. Compensatory masquerade involves replacing impaired functionality with different function that results in the same outcome. For instance, an impaired sense of location can be replaced with remembering directions in order to reach the intended location.

Structural neuroplasticity refers to structural changes (Buonomano & Merzenich, 1998; Demarin & Morovic, 2014; Shaw, 2001). In particular, it allows for permanent physical changes in the neural system due to learning and development. On the individual neuron level psychical changes involve new neural connections, different densities of nerve cells and varying strengths of neural connections. When considering clusters of neurons, physical changes observed are the same as on the individual neuron level but involve clusters of neurons, thus rewiring large regions and reorganizing the nervous system at multiple levels. Moreover, cell assembly theory (Lowel & Singer, 1992) argues that recurring synaptic connections grow more efficient due to stronger nerve connections being established. This dynamic process allows one to learn from and adapt to different experiences. For example, Mechelli et al. (2004) showed that learning a second language increases the density of grey matter in the parietal cortex. They also found that as the fluency increased so did the strength of the structural reorganization. Famously, Maguire et al. (2000) found that London taxi drivers had significantly larger posterior portion of the hippocampus (involved in processing spatial memories) than non-taxi drivers. Moreover, the size of the difference was positively correlated with the amount of time spent as a taxi driver.

As this thesis is interested in the permanent physical changes in neural system due to learning and development, techniques to promote structural neuroplasticity will be employed.

Perceptual training

Perceptual training (simultaneity judgement task) (Powers et al., 2009) involves judging stimuli as simultaneous or non-simultaneous with performance-based feedback being provided. In particular, visual and auditory stimuli are presented with onset asynchronies (SOAs) ranging from - 150ms (auditory stimulus leading) to 150ms (visual stimulus leading) in 50ms intervals. SOAs are presented randomly and not equally distributed (the veridical simultaneous condition had a 6:1 ratio to any of the other 6 non-simultaneous conditions). In this way there is a random and equal likelihood of simultaneous/non-simultaneous conditions, minimizing concerns about response bias. Participants are asked to judge whether the flash and the beep are presented together or separately. They are also informed that they will receive feedback once they have made the response and told to use this feedback to become better at determining whether the flash and the beep occur together or separately. Feedback involves participants being presented with either the phrase `Correct`, green in colour, or `Incorrect`, red in colour. In total perceptual training lasts for approximately an hour.

Perceptual training (Powers et al., 2009) seems to be a technique that is likely to induce structural neuroplasticity given it is based on learning and development. More specifically, the nature of perceptual training is argued to lead to structural neuroplasticity in a form of enhancement of temporal sensitivity, which comes about by shifting the point of subjective simultaneity (PSS – the discrepancy at which two stimuli are perceived as simultaneous) towards the optimum (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019). In other words, perceptual training has shown to modify temporal sensitivity by shifting PSS towards the optimum. That is, the width of the TBW was reduced following perceptual training.

It is also reasonable to speculate that if perceptual training affects temporal sensitivity, then the proposed neural mechanism of temporal sensitivity – alpha peak frequency (Cecere et al., 2015; Hirst et al., 2020; Keil, 2020; Keil & Senkowski, 2017; Migliorati et al., 2020) should similarly be affected. Moreover, if time perception is linked to temporal sensitivity (Droit-Volet, 2008; Fenner et al., 2020; Wang et al., 2005) and alpha peak frequency (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020) it seems that perceptual training is likely to also modify time perception. Similarly, if to assume that temporal sensitivity is affecting SoA (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989) and appears to be linked to the alpha peak frequency (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020) one can conclude that enhancing temporal sensitivity via perceptual training would respectively modify SoA. Despite the likelihood of perceptual training modifying alpha peak frequency, time perception and SoA; the current literature lacks such studies. Therefore, this thesis will focus on examining the effects of perceptual training on the processes in question.

Research aims

The overall aim of this thesis is to investigate the link between alpha oscillations, TBW, time perception and SoA as well as explore their modification via perceptual training.

Experiment 1

In the first experiment we focused on time perception, TBW and frequency of alpha peak. We build on previous research providing some preliminary evidence linking TBW and time perception (Droit-Volet, 2008; Fenner et al., 2020; Wang et al., 2005). In addition, alpha peak frequency has been proposed to be the neural mechanism of TBW (Cecere et al., 2015; Hirst et al., 2020; Keil, 2020; Keil & Senkowski, 2017; Migliorati et al., 2020) and time perception (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020). However, apart from an association between TBW and alpha peak frequency, these links are not well established. Hence, the aim of Experiment 1 was to explore to what degree, if any, time perception, temporal binding window and alpha peak frequency are related.

Experiment 2

In the second experiment we focused on association between TBW and SoA and whether both processes can be modified via alpha tACS. The TBW refers to the time frame within which temporal grouping of sensory information takes place. SoA is the feeling of being in control of one's actions, and their associated outcomes. Given that the temporal grouping of sensory information is an important determinant of SoA (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989), it is plausible that individual differences in TBW are associated with the individual differences in the SoA window. However, existing literature lacks studies exploring this association directly. Therefore, the first aim of this study was to investigate the degree to which individual differences in the TBW correlate with individual differences in the SoA window. The second aim of the experiment was derived from the notion that if temporal grouping of sensory information links TBW with SoA, and given that SoA has been preliminary linked to alpha peak frequency (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020) - the proposed neural mechanism of the TBW (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020), it is plausible that these two processes also have a common underlying neural mechanism – alpha peak frequency.

Experiment 3

The third experiment explored link between TBW and SoA in complex action-outcome relationships involving metacognition of agency. One previous study (Venskus et al., 2021) has shown that the time window of SoA is associated with individual differences in temporal sensitivity when a simple action-outcome relationship is considered. The current study extends this knowledge by exploring how complex action-outcome relationships in metacognition of agency task link to temporal sensitivity.

Experiment 4

The fourth experiment assessed the effects of perceptual training on TBW, SoA and alpha peak frequency. We build on the evidence suggesting perceptual training as an effective means with which to modify temporal sensitivity (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019). More specifically, studies show a reduction in the width of the TBW following perceptual training. However, despite temporal sensitivity being argued to be a fundamental aspect of SoA (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989) the effects of perceptual training on SoA have not been explored. Moreover, the effects of perceptual training on the proposed neural mechanism (alpha peak frequency) of temporal sensitivity (Cecere et al., 2015; Hirst et al., 2020; Keil, 2020; Keil & Senkowski, 2017; Migliorati et al., 2020) also has not been investigated. Therefore, this experiment explored the effects of perceptual training on SoA and alpha peak frequency as well as aiming to replicate observed effects on TBW.

Chapter Two: Individual differences in alpha frequency are associated with the time window of multisensory integration, but not time perception.

This chapter is the accepted version of the paper now published here:

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Abstract

Previous research provides some preliminary evidence to link the temporal binding window, the time frame within which multisensory information from different sensory modalities is integrated, and time perception. In addition, alpha peak frequency has been proposed to be the neural mechanism for both processes. However, these links are not well established. Hence, the aim of the current study was to explore to what degree, if any, time perception, the temporal binding window and the alpha peak frequency are related. It was predicted that as the width of the temporal binding window increases the size of the filled duration illusion increases and the alpha peak frequency decreases. We observed a significant relationship between the temporal binding window and peak alpha frequency. However, time perception was not linked with either of these. These findings are discussed with respect to the possible underlying mechanisms of multisensory integration and time perception.

Keywords: Temporal Binding Window, Occipital Alpha, Time Perception, Double-flash Illusion, Filled Duration Illusion, Multisensory Integration

Introduction

Temporal sensitivity, the ability to detect time-based discrepancy between two stimuli, regulates temporal grouping of sensory information (Colonius & Diederich, 2004). The temporal binding window (TBW) is the time frame within which such grouping takes place and is highly variable across individuals (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). The most often used task to measure the width of the TBW can be argued to be double-flash illusion (for recent reviews see Hirst et al., 2020; Keil, 2020). This task involves simultaneous presentation of visual (flash) and auditory (beep) stimuli followed by the presentation of a second auditory (beep) stimulus after a variable delay. If the second beep occurs within the individuals` TBW then both beeps are integrated with the visual stimulus. This creates an illusion whereby participants report experiencing two flashes despite only one flash being presented. The delay at which an individual no longer perceives two flashes is taken as the width of their TBW, and acts as an index of their temporal sensitivity.

There is evidence suggesting that individual differences in temporal sensitivity are linked with individual difference in time perception. Fenner et al. (2020) measured the width of the TBW, using a simultaneity judgement task, and time perception, using the filled duration illusion. The filled duration illusion is a well-known means to explore time perception (Thomas & Brown, 1974; Wearden et al., 2007; Williams et al., 2019). This task consists of filled intervals that are filled with a continuous tone, and empty intervals that only have the onset and offset signalled with a tone. Evidence robustly shows that filled intervals are judged longer than empty intervals (Plourde et al., 2008), with this effect quantified by the difference in the slope between the filled and empty durations. Fenner et al. (2020) found a positive correlation between the width of the temporal binding window and the magnitude of the filled duration illusion.

If it is the case that individual differences in temporal sensitivity are linked with individual difference in time perception, it is plausible that these two processes also have a common underlying neural mechanism. One strong candidate for this would be the frequency of the occipital alpha peak. The power spectrum of human EEG decreases in amplitude as the frequency increases with an exception around the 10Hz range, where amplitude is increased (see Donoghue et al., 2020 for a comprehensive review). When measured over posterior electrodes, during an awake state, this peak is known as the occipital alpha peak. The precise frequency of this peak varies from one person to the next, normally within the range of 8Hz to 12Hz, but can be as low as 7Hz or as high as 14Hz (Mioni et al., 2020; Zhang et al., 2019).

Alpha oscillations have previously been linked to both the TBW (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020; Samaha & Postle, 2015) and time perception (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020). In terms of TBW, individual differences in the alpha peak frequency have been shown to negatively correlate with the width of the TBW (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020). Moreover, neuromodulation of the alpha peak frequency alters the width of the TBW (Cecere et al., 2015). Namely, decreasing the alpha peak frequency increases the width of the TBW. In terms of time perception Glicksohn et al. (2009) found that the alpha peak frequency correlates with time perception and Horr et al. (2016) found that alpha power has been linked to time perception. In addition, it has been shown that time perception can also be modulated by tACS in the alpha frequency range (Mioni et al., 2020).

The conceptualization behind the link of alpha oscillations with time perception and TBW can be explained by considering internal clock model (a hypothetical mechanism that is driven by a neural pacemaker producing rhythm (Kononowicz & Van Wassenhove, 2016). Treisman (1963) proposed that alpha oscillations in the internal clock drive time perception. Treisman (1963) explained that when the event needing to be timed commences, a pacemaker begins sending pulses. These pulses are then taken as a subjective estimate of elapsed time. Treisman et al. (1994) took this argument further and proposed that the pulses of the pacemaker are driven by alpha oscillations. Similarity, Samaha and Postle (2015) proposed that alpha oscillations in the internal clock drive TBW. Researchers argued that perception depends on the temporal windows, which are clocked by the frequency of the alpha oscillations. Namely, fluctuations in the alpha oscillations predict temporal resolution of perception. A higher alpha frequency provides a narrower excitatory phase, and thus results in a higher temporal sensitivity. In other words, when stimuli are within the same alpha cycle they are perceived as single stimulus. Whereas if stimuli are in different alpha cycles they are perceived as separate. As higher temporal sensitivity gives rise to shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews), this provides a clear link between alpha peak frequency and the TBW. Further support comes from the proposed involvement of alpha oscillations in producing perceptual cycles (Busch et al., 2009; Van Rullen, 2016), whereby the outcome of sensory processing is driven by the phase of alpha oscillations at the time of the presentation of the sensory information.

Despite there being some preliminary findings linking TBW, time perception and alpha oscillations robust conclusions cannot be made. Consequently, the aim of the current study was to investigate to what degree, if any, time perception, TBW and alpha oscillations are linked. Based on the findings described above, it was predicted that an increase in the width of the TBW will be associated with an increase in the size of the filled duration illusion (as in Fenner et al., 2020), and a decrease in alpha peak frequency.

Method

Participants

The sample consisted of 51 student volunteers from the University of Essex recruited via the University`s research advertisement websites. All participants had self-reported normal or corrected to normal vision and hearing to avoid these variables affecting the perception of the tasks. The local ethics committee approved the study, and participants gave their informed consent before taking part in the study. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki and approved by the University of Essex`s Faculty Ethics Subcommittee (departmental reference no: AV1901).

Data Exclusion

All 51 participants took part in the study. The data sets that did not fit the psychometric sigmoid function (R^2 less than .4) or/and contained incomplete data were removed from further analysis. Twelve data sets in the double-flash illusion, two data sets in the filled-duration illusion and one data set in the EEG analysis were removed from the further analysis. Given that some of the participants` data sets were excluded from some tasks but not the others, this resulted in different sample sizes used for different comparisons. Comparison of alpha peak frequency and alpha power with TBW included 38 data sets, alpha peak frequency and alpha power with time perception included 48 data sets and TBW with time perception included 38 data sets.

Design

The study used correlational design with variables being the variability of time perception, the width of the TBW, alpha peak frequency and alpha power.

Apparatus/Materials

<u>Double-flash illusion (TBW measure)</u>

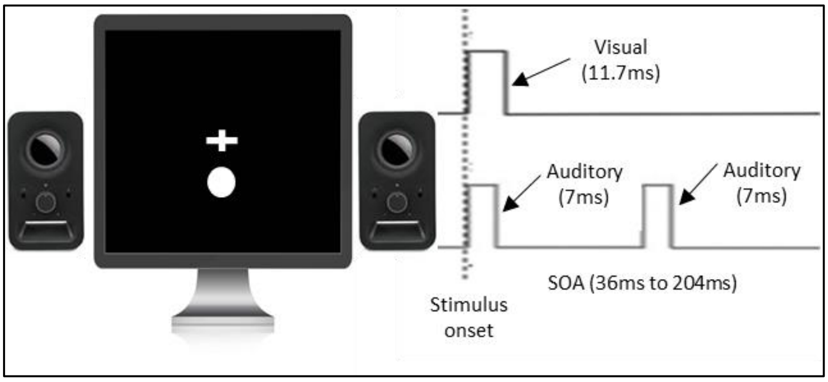

Figure 2.1: Paradigm of the double-flash illusion.

The double-flash illusion task (see Figure 2.1) used was the same as that in the study of Cecere et al. (2015). We chose to use this task, as it has previously been associated with individual differences in the EEG alpha peak frequency, and has also been successfully modulated by tACS and measures the width of the TBW implicitly (Cecere et al., 2015). E-Prime software (Psychology Software Tools, Pittsburgh, PA) and a 17 inch CRT monitor with a refresh rate of 85Hz (ViewSonic Graphics Series G90FB, refresh rate 85Hz) were used to present visual stimuli (flash). Visual stimuli were 11.7ms in duration and in the form of a white circle 1.32cm in diameter. Visual stimuli were located 1cm below the fixation cross that was positioned in the centre of the screen. Such characteristics of stimuli were chosen as it has been shown that tasks involving multisensory integration are optimised when visual stimuli are displayed in peripheral vision (Shams et al., 2002). Auditory stimuli were presented via two typical PC stereo speakers. In order to minimise the possible effect of the spatial cues on the perception of the task, speakers were placed at each side of the monitor and raised to align with the position of the visual stimuli (Macaluso et al., 2004). The auditory stimuli (beep) were presented for 7ms and consisted of a sinusoidal pure tone with a frequency of 3.5kHz and a sampling rate of 44.1kHz played at a constant volume. The above durations of the visual and auditory stimuli were chosen as they have previously been successfully employed to measure multisensory integration (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). The first auditory stimulus was aligned with the onset of the visual stimulus. The second auditory stimulus was presented in one of the possible inter-beep intervals. Inter-beep intervals ranged from 36ms to 204ms in 12ms steps. The above range of inter-beep intervals was chosen as Cecere et al. (2015) showed that such methodology not only captures but also extends beyond the time frame within which the double-flash illusion task is perceived in the general population. Each trial started with a white fixation cross in the centre of the monitor that remained on the screen throughout the trial. On each trial, visual and auditory stimuli were presented simultaneously, with the second auditory stimulus being presented in one of the possible inter-beep intervals randomly. Participants performed one block. Each inter-beep interval was presented 20 times, for a total 300 trials. Participants were instructed to always fixate on the fixation cross and report whether they perceived one or two flashes by pressing the key `1` or the key `2` respectively. Providing a response triggered the start of the next trial. The time interval between the beeps at which participants no longer stated they saw two flashes was calculated to be the width of their TBW.

Filled Duration Illusion (time perception measure)

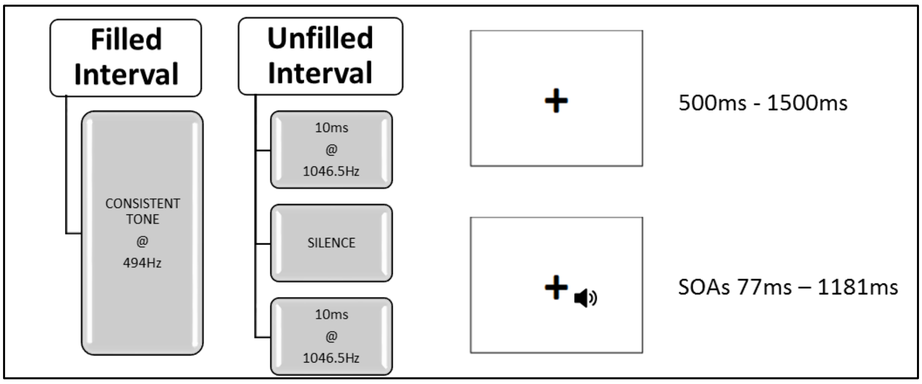

Figure 2.2: Paradigm of filled duration illusion.

The current study used the filled duration illusion (see Figure 2.2) as this method has been shown to be dependable and one of the most frequently used illusions in the time perception field since the beginning (Thomas & Brown, 1974; Wearden et al., 2007; Williams et al., 2019). Furthermore, this task has previously been used to investigate the relationship between time perception and TBW (Fenner et al., 2020). The filled duration illusion refers to the fact that participants experience a filled interval to be longer than an empty interval. A filled interval consists of a single (494Hz) tone presented for the duration of the target interval, and an empty interval encompassed two (1046.5Hz) tones of 10ms presented at the beginning and end of the target interval. The 10 target intervals were 77, 203, 348, 461, 582, 707, 834, 958, 1065 and 1181 in ms. Tones were presented via two typical PC stereo speakers. In order to minimise the possible effect of the spatial cues on the perception of the task speakers were placed at each side of the monitor and their position aligned horizontally with the position of the visual stimuli (Macaluso et al., 2004). Participants completed 5 blocks, each consisting of the 20 stimuli (10 filled and 10 empty) in random order for a total of 100 trials. Each trial was commenced by the participant pressing any button on the keyboard. This triggered the tone/tones. Participants were then asked to estimate the duration of the tone, or the gap between tones, in ms, using the keyboard number pad. Participants were reminded of how ms relate to s (0.5s = 500ms, etc.) and that responses should be within a range of 50ms to 1500ms. Where responses were beyond this range they were discounted and the participant reminded of the possible range.

EEG recording

To measure the alpha peak frequency and alpha power continuous EEG was recorded from 64 sintered Ag/AgCI electrodes mounted on an elastic cap (EasyCap) using a Brain Products BrainAmp DC system throughout the tasks. Left mastoid was used as a reference during recording.

Procedure

Participants were seated in a dimly lit room with their corporeal midline aligned with a centre of the computer screen located approximately 60cm away. Participants then signed a consent form and were given opportunity to enquire about the study. Thereafter participants performed flash-beep illusion task (10 minutes) followed by the filled duration illusion task (20 minutes) while EEG was recorded.

Data Analysis

<u>TBW</u>

To assess the width of the TBW, the time window in which the illusion was maximally perceived, the percentage of trials where two flashes were reported was first plotted as a function of the inter-beep delay. A psychometric sigmoid function was then fitted to the data. The sigmoid function was defined by the equation: $y = a+b/(1+\exp(-(x-c)/d))$ (a = upper asymptote; b = lower asymptote; c = inflection point; d = slope). For each participant, c was taken as the TBW, i.e. the point of decay of the illusion (Cecere et al., 2015).

<u>Time Perception</u>

To determine the variability in time perception, for each participant the regression between participants' estimated times and the actual intervals were calculated in the filled duration illusion task. The difference between the filled and empty slopes in filled duration illusion task was taken as a measure of the size of the filled duration effect, corresponding to the individual differences in time perception (as in Fenner et al., 2020).

<u>Alpha Oscillations</u>

For each of the two tasks, data were extracted in one second epochs corresponding to the second immediately prior to stimulus presentation. For eyes open and eyes closed resting data, the 120 second periods were divided into epochs of one second. Bad channels were removed by visual inspection. Noisy epochs were excluded using automatic artifact rejection in eeglab (Delorme & Makeig, 2004), with the joint probability parameter and kurtosis parameter set to 5, and amplitude threshold set to 5000. Independent component analysis in eeglab (Delorme & Makeig, 2004) was used to identify and remove eye blinks. A second round of artifact rejection was then completed with the joint probability parameter and kurtosis parameter set to 5, and amplitude threshold set to 2000. Each one second window was then multiplied by a Hanning taper, and zero-padded to 10s. Power was computed from 4Hz to 30Hz using a fast Fourier transform (FFT function in matlab). The resulting FFT had a frequency resolution of 0.1Hz. The power at each frequency was normalising by subtracting the mean power across the spectrum, and dividing by the standard deviation (see Singh et al., 2015 for a similar approach).

To determine alpha peak frequency, we found the maximum power between 8Hz and 14Hz. Based on previous studies, we extracted the alpha peak frequency averaged across 6 posterior electrodes (Oz, O1, O2, PO3, POZ and PO4). Here, we present only analysis from during the tasks, but analysis during rest with eyes closed and eyes open provides a similar pattern of the results. Data are available at: https://doi.org/10.17605/OSF.IO/VAW7D. Although we were primarily interested in alpha peak frequency, we additionally calculated alpha power. To do this we calculated the mean amplitude of the power spectrum between 8Hz and 14Hz over the pooled posterior electrodes (Oz, O1, O2, PO3, POZ and PO4).

Results

Relationship of alpha peak frequency with TBW during double-flash illusion task.

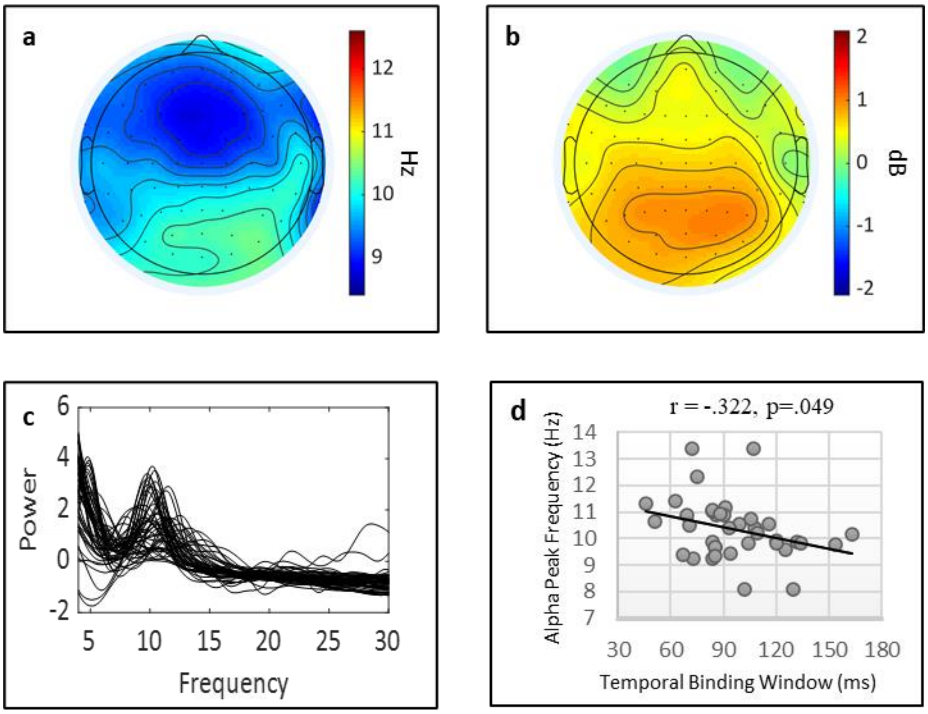

Figure 2.3: (a) Topographic distribution of the frequency of the alpha peak for each electrode during double-flash illusion task across all participants. The power spectrum has a lower peak at frontal electrodes, whereas over posterior electrodes this peak is at around 11Hz. (b) Topographic distribution of the alpha power, for each electrode during double-flash illusion task across all participants. (c) Power spectrum over posterior electrodes during the double-flash illusion task for each participant. (d) Scatterplot showing relationship between the alpha peak frequency and the temporal binding window. Alpha peak frequency decreases as the width of the temporal binding window increases.

The scatterplot (see Figure 2.3 d) indicated that there was a linear relationship between the alpha peak frequency (Hz) (α = 0.97) and the width of the TBW (ms) (α = 0.99). This was confirmed with a Pearson's correlation coefficient, $r(36)=-.32, p=.049$, which showed weak to moderate strength significant correlation. The slope coefficient for alpha peak frequency was -7.53, so the width of the TBW decreases by 7.53ms for each increase in Hz in alpha peak frequency. No association was found between alpha power (dB) (α = 0.97) and the width of the TBW (ms) (α = 0.99) during the double-flash illusion task, $r(36)=-.09, p=.600$. A sensitivity power analysis demonstrated that our sample had 80% power to detect moderate correlation of 0.44 or greater (α=.05, two-tailed).

Relationship of alpha peak frequency with time perception during filled duration illusion task.

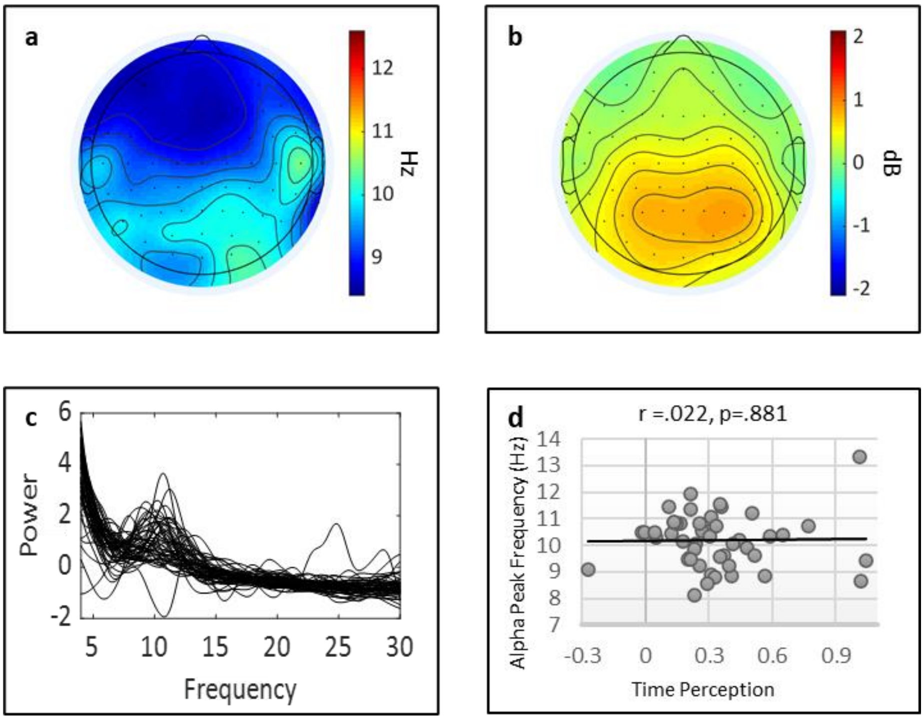

Figure 2.4: (a) Topographic distribution of the frequency of the alpha peak for each electrode during filled duration illusion task across all participants. The power spectrum has a lower peak at frontal electrodes, whereas over posterior electrodes this peaks at around 10 Hz. (b) Topographic distribution of the alpha power, for each electrode during filled duration illusion task across all participants. (c) Power spectrum over posterior area during filled duration illusion task for each participant. (d) Relationship between the alpha peak frequency and the time perception. Alpha peak frequency and time perception have a non-significant relationship. (The time perception represents the magnitude of the filled duration illusion effect by displaying the difference in filled and empty slopes. A positive value indicates that the filled slope was steeper than the empty slope and vice versa.).

The scatterplot (see Figure 2.4 d) indicated that there was no apparent relationship between the alpha peak frequency (Hz) (α = 0.97) and time perception (the difference in slopes between the filled and empty duration estimates). This was confirmed with a Pearson's correlation coefficient, *r(46)=.02,p=.881*, which showed non-significant correlation. No association was found between alpha power (dB) (α = 0.97) and time perception (α = 0.98) during the filled duration illusion, *r(46)=.16,p=.264*. A sensitivity power analysis demonstrated that our sample size had 80% power to detect moderate correlation of 0.39 or greater (α=.05, two-tailed).

Relationship between temporal sensitivity and time perception

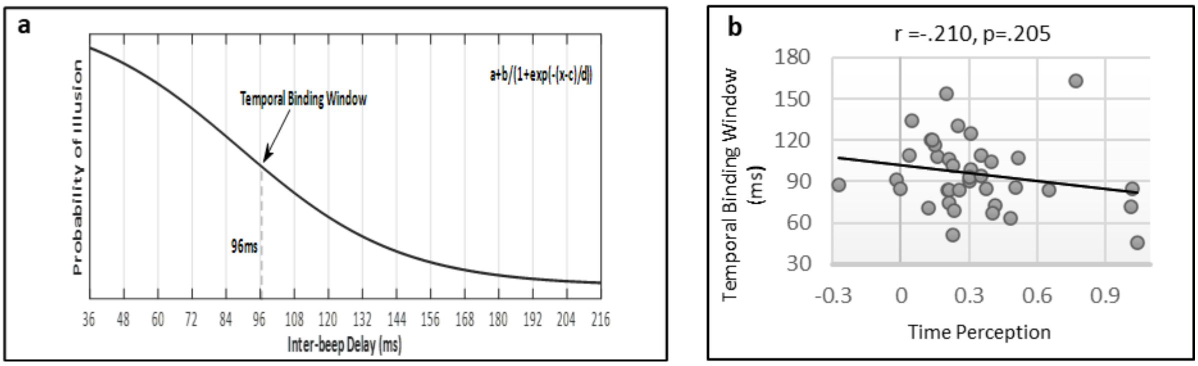

Figure 2.5: (a) Across-participants average probability of perceiving the double-flash illusion plotted as a function of inter-beep delay. The curve represents the sigmoid fit determining the point of decay of the illusion, corresponding to the width of the TBW. (b) Relationship between temporal sensitivity and time perception. Temporal sensitivity and time perception are shown to have non-significant relationship.

The scatterplot (see Figure 2.5 b) showed that there was no apparent relationship between the width of the TBW (ms) (α = 0.99) and the time perception (α = 0.98). This was confirmed with a Pearson's correlation coefficient, *r(36)=-.21,p=.205*, which showed non-significant correlation. A sensitivity power analysis demonstrated that our sample had 80% power to detect moderate correlation of 0.44 or greater (α=.05, two-tailed).

Discussion

Findings

The key aim of the current study was to investigate the relationship between temporal sensitivity, time perception and alpha peak frequency. It was predicted that an increase in the width of the TBW would be associated with an increase in the size of the filled duration illusion and decrease in alpha peak frequency. However, the results showed a significant relationship (negative correlation) only between the width of the TBW and the alpha peak frequency. Additionally, the current study explored relationship of alpha power with the temporal sensitivity and time perception, with the results indicating non-significant relationship between these processes.

Link with previous literature

Given the above results it is evident that the current study supports previous findings (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020; Samaha & Postle, 2015) indicating that the TBW and the alpha peak frequency are related. However, only one study (Cecere et al., 2015) with a very small sample size (12 participants) have showed causal evidence (the alpha peak frequency modulates the width of the TBW). As the current study is the only study since Cecere et al. (2015) that has investigated this phenomenon, it provides the opportunity to reaffirm these findings with more confidence. Additionally, the current study found no association between the TBW and alpha power. These findings support previous literature regarding relationship between alpha peak frequency and alpha power. Alpha peak frequency and alpha power have been shown to be somewhat related overall, but when investigated in detail (i.e. independent component analysis) only very few aspects were shown to be associated (Benwell et al., 2019). Hence the above, taken together with the current results concerning relationship of alpha peak frequency and alpha power with TBW, further supports the notion that alpha power and alpha frequency are distinctive. Moreover, these findings allow to conclude that TBW is linked to alpha peak frequency but not alpha power.

However, the current study contradicts findings of Fenner et al. (2020), demonstrating a relationship between the TBW and the time perception, as well as findings of Glicksohn et al. (2009), Horr et al. (2016) and Mioni et al. (2020), suggesting that time perception is related to the alpha peak frequency and alpha power.

In terms of the discrepancy between the current results and those of Fenner et al. (2020) it seems that methodology, in particular the tasks used, may be the possible reason for the conflicting results obtained. Both Fenner et al. (2020) and the current study examined time perception using filled duration illusion where participants were asked to estimate in ms how long a sound is played for (the filled interval), or what the interval was between two sounds (the empty interval). This resulted in conscious thinking about time. However, the two studies used different tasks to assess the width of the TBW. Namely, Fenner et al. (2020) used the simultaneity judgement task whereas current study used the double-flash illusion task to assess the width of the TBW. The simultaneity judgement task and the double-flash illusion task both employed simple stimuli (flashes and beeps). Such stimuli result in integration only across modalities and hence allow for accurate and reliable investigation of across modalities integration. Similarly, both tasks used various time delays between the stimuli. In the simultaneity judgment task participants are presented with either a flash leading followed by the beep with various time delays or vice versa. In double-flash illusion task participants were presented with two beeps separated by various time intervals and a flash aligned with the first beep. TBW is the time frame within which stimuli are integrated and hence various intervals between the stimuli are needed to allow the assessment of the integration of the stimuli and consequently the width of the TBW. On the surface it seems that both tasks assess the width of the TBW similarly.

However, one difference between the tasks is the processes involved in responding to the question of the task. More precisely, in the simultaneity judgement task participants need to decide whether the two stimuli occur at the same time or not. The time interval at which participants perceive the two stimuli to be occurring at different times is said to be the person`s TBW. In the double-flash illusion task participants are required to decide whether they saw one or two flashes. The time interval between the beeps at which participants no longer stated they saw two flashes is used to measure the width of their TBW. As stated before, to provide a response to the simultaneity judgement task participants must decide whether the two stimuli (flash and beep) occurred at the same time. Hence, it is likely that during the judgement, not only the implicit process of integrating multisensory information is involved, but also the more explicit process of time perception is involved. More specifically, in the simultaneity judgement task an implicit process of integrating multisensory information occurs due to stimuli (flash and beep) being integrated if within the TBW. More explicit processing of temporal structure also occurs in this task as participants are directly instructed to determine whether or not flash and beep occur at the same time, resulting in participants consciously thinking about time between the stimuli. Hence, it seems that the simultaneity judgement task used to assess the width of the TBW and filled duration illusion used to assess the time perception both involve a common underlying process, namely thinking about time. If the above is to be true it perhaps could explain why there was a relationship found between TBW and time perception in Fenner et al. (2020) study.

In contrast, to provide response to the double-flash illusion task only implicit process of integration of multisensory information seems to occur. Namely, here participants must rely on this process solely as they are asked to only concentrate on the number of the flashes perceived and hence no conscious thinking about time is involved. Given the above, it seems that the relationship between time perception and the temporal binding window observed in Fenner et al. (2020) might be in part due to the fact that the two tasks shared a common underlying process, where both tasks required explicitly thinking about time. When one of the measures are assessed implicitly, as in the current study assessing the width of the TBW with double-flash illusion, this association seems to be less observable. Future research should explore this possibility in more detail. Additionally, different time perception and TBW tasks also should be investigated. Different tasks potentially could measure different phenomenon as shown above (i.e. explicit vs implicit).

With respect to the link between the time perception and the alpha oscillations, it is evident that the data does not align with the existing literature. The current findings contradict results obtained by Horr et al. (2016) and Glicksohn et al. (2009) suggesting relationship between time perception and alpha oscillations. The study by Glicksohn et al. (2009) used much longer time intervals (up to 32s) than those employed in the current study (up to 1181ms), which raised the possibility that participants used chronometric counting. Hence it could be argued that the relationship between the alpha peak frequency and time perception is being mediated by the chronometric counting (Bizo et al., 2006) in Glicksohn et al. (2009) study. While Horr et al. (2016) used similar intervals to those employed in the current study, these intervals were filled with regularly spaced tones, whereas we used either entirely filled or empty durations. Further research is required to fully understand why this difference might be crucial to the correlation with alpha oscillations, but one possibility is that the task in Horr et al. (2016) triggers neural entrainment that can drive distortions in time perception (Matthews et al., 2014), and that these in turn might be mediated by alpha oscillations.

Conclusions and significance of the results

The aim of the current study was to investigate to what degree, if any, time perception, the TBW and the alpha peak frequency are linked. We found no evidence to support a link between time perception and the TBW or alpha peak frequency. Despite the above findings contrasting with existing literature, they provide significant and novel conclusions upon which to build further studies. In line with previous research, we found evidence in support of the link between alpha peak frequency and the TBW. This finding confirms the role of alpha oscillations in driving the time window of sensory integration.

Chapter Three: Temporal binding window and sense of agency are related processes modifiable via occipital tACS.

The data from this chapter are now published as experiment 3 in the following paper:

Venskus, A., Ferri, F., Migliorati, C., Spadone, S., Costantini, M., & Hughes, G. (2021). Temporal binding window and sense of agency are related processes modifiable via occipital tACS. PlosOne, https://doi.org/10.1371/journal.pone.0256987.

This chapter has been written up here as a stand-alone experiment that follows on from the first two experiments described in the reference above. These previous experiments are referred to as “Venskus et al., 2021; experiment 1 and 2” in the current chapter.

Abstract

The temporal binding window refers to the time frame within which temporal grouping of sensory information takes place. Sense of agency is the feeling of being in control of one's actions, and their associated outcomes. While previous research has shown that temporal cues and multisensory integration play a role in sense of agency, only one previous study has directly assessed whether individual differences in the temporal binding window and sense of agency are associated. The current study aimed to accumulate evidence in relation to the degree to which individual differences in the temporal binding window correlate with individual differences in the sense of agency window. To assess sense of agency, participants pressed a button triggering, after a varying delay, the appearance of the circle, and reported their sense of agency over the effect. To assess the temporal binding window a double-flash illusion was performed. Unexpectedly, the temporal binding window and the sense of agency window were shown not to be associated. However, both of these processes were modulated by applying occipital tACS at either 14Hz or 8Hz. We found 14Hz tACS stimulation was associated with narrower temporal biding window and sense of agency window. Overall, our results suggest the temporal binding window and the time window of sense of agency are related. They also point towards a possible underlying neural mechanism (alpha peak frequency) for this association.

Keywords: Temporal Sensitivity, Occipital Alpha Peak Frequency, Sense of Agency Window, Double-flash Illusion, Multisensory Integration

Introduction

Temporal grouping of sensory information is dependent on temporal sensitivity, in other words the ability to detect a time-based discrepancy between two stimuli (Colonius & Diederich, 2004). The time frame within which temporal grouping of sensory information takes place is known as the temporal binding window (TBW). This window is highly variable across individuals (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). Recent reviews (Hirst et al., 2020; Keil, 2020) of the literature have shown that double-flash illusion is often used to explore the TBW. This task involves simultaneous presentation of visual (flash) and auditory (beep) stimuli followed by the presentation of a second auditory (beep) stimulus after a variable delay. If the second beep occurs within the individual's TBW then both beeps are integrated with the visual stimulus. This creates an illusion whereby participants report experiencing two flashes despite only one flash being presented. The delay at which an individual no longer perceives two flashes is taken as the width of their TBW, and acts as an index of their temporal sensitivity (see Hirst et al., 2020; Keil, 2020).

There is also evidence suggesting that temporal grouping of sensory information plays a pivotal role in sense of agency (SoA) (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). SoA refers to the feeling of being in control of one's actions and their associated outcomes (i.e. the feeling of having caused a sensory event in the environment). Previous studies have shown that increasing the interval between an action and an associated sensory outcome leads to a reduction in SoA (Shanks et al., 1989). In addition, SoA seems to depend on temporal grouping of actions and outcomes. For instance, SoA for an outcome can be reduced by the presence of an additional sensory event coinciding with the action because this event, rather than the outcome, is integrated with the action (Kawabe et al., 2013). Farrer et al. (2013) proposed that if action and outcome occur within a specific temporal interval, within which the action and the outcome are integrated, one experiences a greater SoA. In their study, participants were required to perform an action (a button press) that elicited an outcome (apparition of a circle on a screen) with various delays and to report their sense of agency over that outcome. Findings indicated that participants were more likely to report SoA for the outcome at shorter delays as opposed to longer delays, supporting the notion that SoA depends on the temporal relationship between action and outcome.

Given that temporal grouping of sensory information is an important determinant of SoA, it is plausible that individual differences in TBW are associated with the individual differences in the SoA window. As both phenomena are linked by temporal grouping of sensory information, a positive association would be expected. However, existing literature lacks studies exploring this association directly with only one study (Venskus et al., 2021; experiment 1 and 2) to date undertaking such investigation. More specifically, Venskus et al. (2021; experiment 1 and 2) showed that TBW positively correlate with SoA. Therefore, the first aim of the current studies is to replicate Venskus et al. (2021; experiment 1 and 2) study to accumulate evidence in relation to the degree to which individual differences in the TBW correlate with individual differences in the SoA window.

If temporal grouping of sensory information links the TBW and SoA, it is plausible that these two processes also have a common underlying neural mechanism. One strong candidate for this would be the frequency of the occipital alpha peak. The power spectrum of human EEG broadly decreases in amplitude as the frequency increases, with some additional peaks at various frequencies, most notably at around 10Hz (see Donoghue et al., 2020 for a comprehensive review). When measured over posterior electrodes, during awake state, this peak is known as the occipital alpha peak. The precise frequency of this peak varies from one person to the next, normally within the range of 8Hz to 12Hz, but can be as low as 7Hz or as high as 14Hz (Mioni et al., 2020; Zhang et al., 2019).

In terms of the TBW, a higher alpha frequency provides a narrower excitatory phase, and thus results in a higher temporal sensitivity, allowing detection of a shorter temporal discrepancy between two stimuli. As higher temporal sensitivity gives rise to shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews), this provides a clear link between alpha peak frequency and the TBW. Studies directly investigating alpha peak frequency and TBW provide further support for this assumption. For example, individual differences in the frequency of the alpha peak have been found to correlate negatively with the width of the TBW (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020). Furthermore, neuromodulation (via tACS) of the frequency of the occipital alpha peak alters the width of the TBW accordingly (increased frequency of the occipital alpha peak is associated with decreased width of the TBW; Cecere et al., 2015).

With regards to SoA, the evidence of a possible link to alpha peak frequency is less direct. Nonetheless, as highlighted above, SoA is highly dependent on the interval between action and outcome. Recent evidence has shown that time perception is linked to the TBW (Fenner et al., 2020) and can also be modulated by tACS in the alpha frequency range (Mioni et al., 2020). These studies suggest that alpha peak frequency may act as a kind of “sample rate” to the visual system, influencing both sensory integration at short intervals (corresponding to an alpha cycle) as well as time perception at longer intervals. As such, if SoA depends in part on the time interval between action and outcome, and on the perception of this interval, then it follows that SoA might also relate not just to the TBW but also to peak alpha frequency. Therefore, the second aim of the current study is to explore whether occipital tACS stimulation alters the width of the SoA window as well as the TBW.

We first investigated the link between the SoA window and the TBW. Participants performed a judgment of agency task (Farrer et al., 2013) and double-flash illusion task (Cecere et al., 2015; Shams et al., 2002). The judgment of agency task allowed us to obtain a measure of the

SoA window, while the double-flash illusion task provided a measure of the TBW. Secondly, we explored whether the frequency of the occipital alpha peak is related to TBW and SoA. That is whether the tACS stimulation at the upper and lower bounds of the frequency of the occipital alpha peak alters the width of the SoA window similarly to width of the TBW.

Method

Participants

The sample consisted of 45 participants, as per the preregistration. Participants consisted of student volunteers from the University of Essex recruited via the University research advertisement websites. All participants had normal or corrected to normal vision and hearing to avoid these variables influencing the tasks. The local ethics committee approved the study, and participants gave their informed consent before taking part in the study. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki and approved by the University of Essex`s Faculty Ethics Subcommittee (departmental reference no: AV1901). The study was preregistered on AsPredicted, accessible via https://aspredicted.org/dh38n.pdf. Data is made accessible on OSF via the following link: https://osf.io/d7rwu/?view_only=9bc4321f99ce4c179f5aacd49c65c0aa.

Exclusion Criteria

In total 45 participants took part in the study and consisted of 35 females and10 males (age: M=21.8, SD=5.9). The data of those participants that failed to complete the entire study or failed to perceive the double-flash illusion task (not experiencing the illusion on any of the trials) was removed from further analysis. Similarly, as per the preregistration, those data sets that did not fit the psychometric sigmoid function (R^2 less than .4) were removed from further analysis. After exclusion, the SoA task included a final sample of 33 data sets that consisted of 26 females and 7 males (age: M=22.2, SD=6.4), while the TBW task included a final sample of 32 data sets that consisted of 25 females and 7 males (gage: M=20.7, SD=3.4).

Design

The current study used a within-subjects design. The independent variable in the study was the tACS stimulation at 2 frequencies (8Hz and 14Hz). All participants experienced both frequencies of the tACS stimulation. The order of the tACS sessions was counterbalanced, such that half of the participants completed the 8Hz condition first while the other half completed 14Hz condition first. The dependent variables were the width of the TBW and the width of the SoA window measured at both frequencies.

Apparatus/Materials

<u>tACS stimulation</u>

tACS was delivered by a battery-powered DC stimulator (Magstim, UK) via two rubber electrodes enclosed in saline-soaked sponges. Sponges containing the electrodes were imbedded into an EEG cap to keep the electrodes securely attached on the head. The reference electrode was located on the vertex (Cz), whilst the stimulation electrode was located on the occipital cortex (Oz). In order to decrease the current density at the reference location, the reference electrode was 35cm^2 whereas stimulation electrode was 9cm^2. A sinusoidal waveform current was used, the DC offset was set at 0, the intensity of the stimulation was set at 2 mA peak to peak (10 seconds fade in) and the impedance was set below 5k. The above protocol is a replication of the protocol employed by Cecere et al. (2015).

<u>Double-flash illusion (TBW measure)</u>

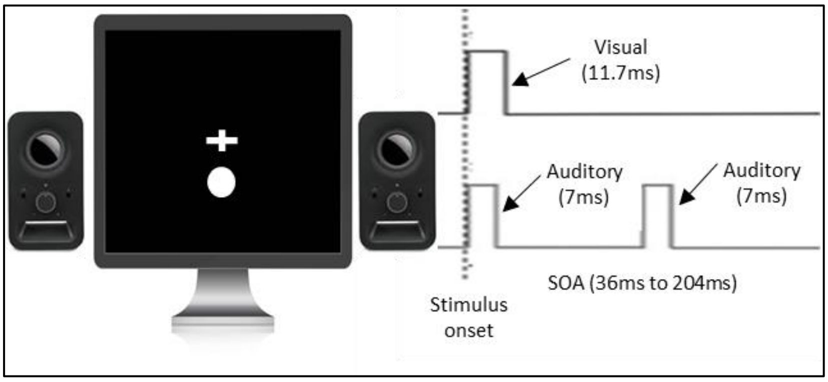

Figure 3.1: Paradigm of the double-flash illusion.

The double-flash illusion task (see Figure 3.1) used was the same as that in the study of Cecere et al. (2015), and in the first study presented in this thesis. We chose to use this task, as it has previously been associated with individual differences in the EEG alpha peak frequency and has also been successfully modulated by tACS and measures the width of the TBW implicitly (Cecere et al., 2015). E-Prime software (Psychology Software Tools, Pittsburgh, PA) and a 17 inch CRT monitor with a refresh rate of 85Hz (ViewSonic Graphics Series G90FB, refresh rate 85Hz) were used to present visual stimuli (flash). Visual stimuli were 11.7ms in duration and in the form of a white circle 1.32cm in diameter. Visual stimuli were located 1cm below the fixation cross that was positioned in the centre of the screen. Such characteristics of stimuli were chosen as it has been shown that tasks involving multisensory integration are optimised when visual stimuli are displayed in peripheral vision (Shams et al., 2002). Auditory stimuli were presented via two typical PC stereo speakers. In order to minimise the possible effect of the spatial cues on the perception of the task, speakers were placed at each side of the monitor and their position raised to aligned with the position of the visual stimuli (Macaluso et al., 2004). The auditory stimuli (beep) were presented for 7ms and consisted of a sinusoidal pure tone with a frequency of 3.5kHz and a sampling rate of 44.1kHz played at a constant volume. The duration of the visual and auditory stimuli was chosen as they have previously been successfully employed to measure multisensory integration (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). The first auditory stimulus was aligned with the onset of the visual stimulus. The second auditory stimulus was presented in one of the possible inter-beep intervals. Inter-beep intervals ranged from 36ms to 204ms in 12ms steps. The above range of inter-beep intervals was chosen as Cecere et al. (2015) showed that such methodology not only captures but also extends beyond the time frame within which the double-flash illusion task is perceived in the general population. Each trial started with a white fixation cross in the centre of the monitor that remained on the screen throughout the trial. On each trial, visual and auditory stimuli were presented simultaneously, with the second auditory stimulus being presented in one of the possible inter-beep intervals randomly. Participants performed one block. Each inter-beep interval was presented 20 times, for a total 300 trials. Participants were instructed to always fixate on the fixation cross and report whether they perceived one or two flashes by pressing the key `1` or the key `2` respectively. Providing a response triggered the start of the next trial. The time interval between the beeps at which participants no longer stated they saw two flashes was calculated to be the width of their TBW.

Judgement of agency task (SoA window measure)

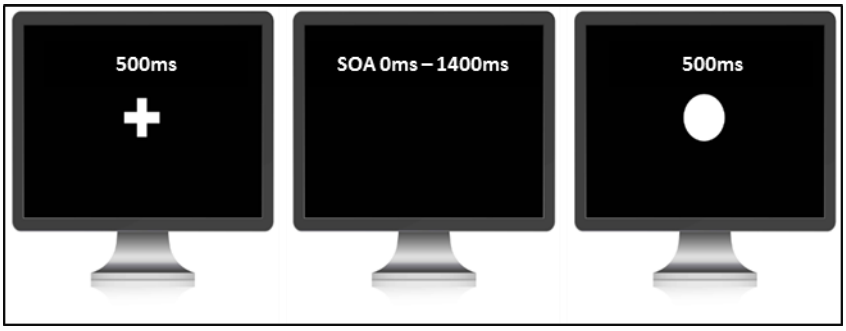

Figure 3.2: Paradigm of the judgement of agency task.

The judgement of agency task (see Figure 3.2) was adapted from Farrer et al. (2013). All stimuli were presented using MATLAB running Psychtoolbox extension (Brainard, 1997; Kleiner et al., 2007) on an LCD monitor with a refresh rate of 60Hz. Each trial started with a white fixation cross in the centre of the monitor. After a delay of 1500ms the fixation cross disappeared, signalling the beginning of the trial. After the cross disappeared, participants were asked to press the space bar on the computer keyboard whenever they wanted. Once participants pressed the key, a grey circle of 2.5cm in diameter was displayed in the centre of the screen for 500ms with 11 possible delays ranging from 0ms to 1400ms in steps of 140ms. The task consisted of 2 blocks with each delay being presented 10 times in random order. In total participants completed 220 trials. Participants were required to judge if the appearance of the circle was caused by their button press, or if the computer had triggered the circle to appear. Participants were told that on some trials the computer would cancel their button press and re-trigger the appearance of the circle at a random interval. Participants needed to press key `1` if they thought that it was most likely they triggered the circle to appear and `2` if they thought that it was most likely computer triggered the circle to appear. This response approach was chosen over that of that of Farrer et al. (2013), where participants were given three choices (i.e. full control, partial control and no control), to avoid participants opting for the partial control if not fully sure. Such partial control responses would complicate the calculation of the time window of SoA, via the fitting of a sigmoid function.

Procedure

Before undertaking the study tACS intensity was adjusted to each participant individually. Namely, tACS intensity was initially set to 2000 μA reduced until the participant no longer experience phosphenes. Thresholds ranged from 1600 μA to 2000 μA. Participants were seated in a dimly lit room approximately 60cm away from the computer screen with the plane of their eyes aligned to the centre of the monitor. Participants completed the double-flash illusion and the judgement of agency task while receiving continuous tACS at 8Hz or 14Hz. Approximately a week (7 +/- 1 day) after the initial tasks participants completed the same two tasks while receiving continuous tACS at 8Hz or 14Hz depending which frequency of occipital alpha cycle was used previously. The order of the tasks was counterbalanced across participants.

Data Analysis

To examine the SoA window, the number of times the individual reported that they caused the circle to appear on the screen was recorded. Thereafter, a sigmoid function was fitted to the data, determining each participant`s inflection point (corresponding to the width of the SoA window), in ms. A decreasing sigmoid function was used to fit the distribution of responses and was defined by the equation: $y = a+b/(1+\exp(-(x-c)/d))$ (a = upper asymptote; b = lower asymptote; c = inflection point; d = slope). For each participant, c was taken as the SoA window, i.e. the point of decay of the self-attribution (Sato, 2009; Shimada et al., 2010). To assess the width of the TBW, the time window in which the illusion was maximally perceived, the percentage of trials where two flashes were reported was first plotted as a function of the inter-beep delay. A psychometric sigmoid function was then fitted to the data. The sigmoid function was defined by the equation: $y = a+b/(1+\exp(-(x-c)/d))$ (a = upper asymptote; b = lower asymptote; c = inflection point; d = slope). For each participant, c was taken as the TBW, i.e. the point of decay of the illusion (Cecere et al., 2015).

Results

Effect of occipital tACS stimulation on TBW and SoA window

By examining the group averaged raw data and the sigmoid curve it appears that the width of the TBW and the width of the SoA window is wider at 8Hz condition than 14Hz condition (see Figure 3.3).

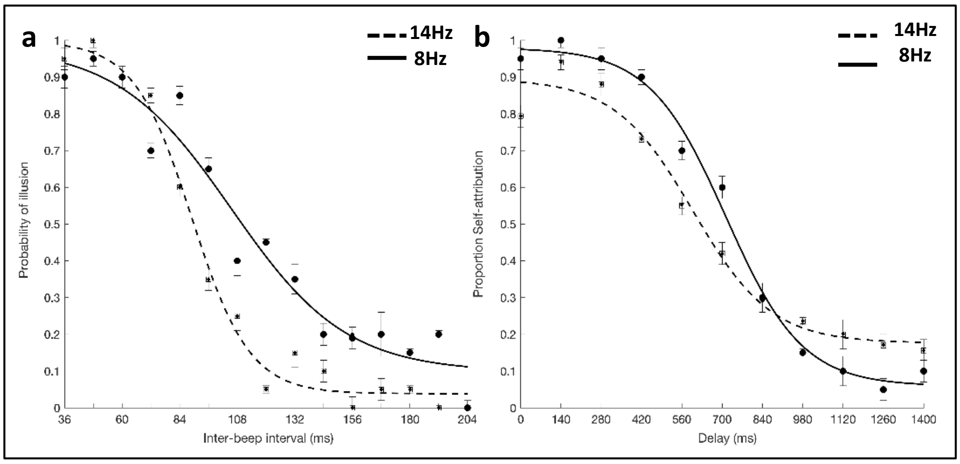

Figure 3.3: (a) Average percentage of probability of perceiving the illusion plotted as a function of inter-beep delay. A sigmoid function was then fitted to the averaged data points. The curve represents the sigmoid fit determining the point of decay of the illusion, corresponding to the width of the TBW. The points represent across-participants average raw data. (b) Average percentage of probability of self-attribution plotted as a function of delay. Data of each participant was first averaged for each delay and hereafter across all participants according to the delays. A sigmoid function was then fitted to the averaged data points. The curve represents the sigmoid fit determining the point when the SoA judgement changes, corresponding to the width of the SoA window. The points represent across-participants average raw data.

A paired-samples t-test confirmed that the width of the TBW was wider at 8Hz (M=108ms, SD=25ms) than 14Hz (M=91ms, SD=28ms), *t(31)=3.2,p=.003*, d=0.64, observed power 0.88. A sensitivity power analysis showed that our sample size had 80% power to detect medium effect sizes for t tests (dz=0. 52, α=.05, two-tailed). Similarly, a paired-samples t-test showed that the width of SoA window was wider at 8Hz (M=700ms, SD=266ms) than 14Hz (M=605ms, SD=268ms), *t(32)=2.2,p=.034*, d=0.36, observed power=0.58. A sensitivity power analysis showed that our sample size had 80% power to detect medium effect sizes for t tests (dz=0. 50, α=.05, two-tailed). Taken together these findings suggest that tACS stimulation at the upper or lower bounds of the frequency of the occipital alpha peak, alters the width of the SoA window similarly to width of the TBW.

Relationship between TBW and SoA window

To test whether the SoA window is related to the TBW a correlation between the above variables was conducted. We conducted separate correlations within each stimulation session to assess the relationship between the SoA window and the TBW. Results of the Pearson correlation indicated that there was no relationship between the width of the TBW ($\alpha = 0.99$) and SoA window ($\alpha = 0.99$) in 8Hz condition, $r(28)=-.06, p=.758$, or between the width of the TBW ($\alpha = 0.99$) and SoA window ($\alpha = 0.99$) in the 14Hz condition, $r(28)=.29, p=.133$. A sensitivity power analysis demonstrated that our sample size had 80% power to detect moderate correlation of 0.49 or greater ($\alpha=.05$, two-tailed).

Discussion

One of the aims of the current study was to explore the relationship between the TBW and SoA. As both phenomena are linked by temporal grouping of sensory information, it was predicted that a positive correlation would be found. Another aim was to explore whether the tACS stimulation at the upper and lower bounds of the frequency of the occipital alpha peak alters the width of the SoA window and TBW.

Relationship between TBW and SoA window

With respect to the direct relationship between the TBW and SoA window, this study was the second to directly address this question. While the first study (Venskus et al., 2021; experiment 1 and 2) provide support for the link between these two processes, this relationship was not observed in the current study. How might we understand this inconsistent pattern of results? Although an important aspect of both TBW and SoA window is the temporal grouping of sensory information, this connection is stronger for the TBW compared to SoA window. Indeed, SoA is known to be modulated by many different cues (Chambon et al., 2014; Moore & Fletcher, 2012), whereas TBW is purely a measure of temporal sensitivity. More specifically, in addition to the temporal relationship between action and outcome, SoA can also be influenced by action selection fluency (Chambon et al., 2014; Wenke et al., 2010) as well as the consistency between the predicted and the actual outcome. The former refers to a notion that SoA is influenced by the action selection in advance of the action itself, and before action outcomes are known (Chambon & Haggard, 2012). In the latter case, this can be explained both in terms of predictive processes (Frith et al., 2000), and in terms of postdictive confabulation (Wegner, 2002). This calculation might also include integrating prior information to inform our SoA (Moore & Fletcher, 2012). Such prior information may include (but might not be limited to) possible alternative causes of the observed action outcome, or whether or not the action was freely selected. As such, although SoA is likely informed by cues related to temporal integration, and therefore will relate to the TBW, this relationship will inevitably be incomplete. Hence, although linked, SoA and TBW are also partially dissociable.

Given the fact that SoA depends on many different cues, one might also expect this to vary in different contexts, and also between individuals (Sidarus et al., 2017). In latter case for instance, some participants might rely more on temporal cues, and less on action-related, or other cues. With respect to different contexts, we must mention that one important difference in the current study compared to Venskus et al. (2021; experiment 1 and 2) study is that participants were undergoing continuous tACS stimulation while completing the judgement of agency task. As such, it is possible that the presence of tACS stimulation may have been responsible for removing the association between TBW and SoA window. This could occur either directly, as a result of stimulating the brain, or indirectly, as a result of the change in context. Indeed, previous research has shown that electrical brain stimulation can alter the degree to which participants integrate information about action-outcome congruency when generating judgements of agency (Hughes, 2018). Indirect effects might be less prevalent in the double-flash illusion task, which predominately utilises temporal cues. Further research should investigate this possible explanation in more detail, for instance by including additional baseline conditions and/or sham stimulation conditions.

It is also worth noting that the current study used a slightly different version of the double-flash illusion task than did Venskus et al. (2021; experiment 1 and 2). We chose this version of the task as it has previously been successfully modulated by tACS (Cecere et al., 2015). Although the different tasks used to measure TBW share many common features and are grounded in the same theoretical framework, subtle differences between the tasks may lead to slight differences in the degree to which they correlate with the SoA window. Hence, further research should also explore the possibility that the relationship between TBW and SoA window vary somewhat dependent on the precise task features. Nonetheless, the association observed between these two processes in Venskus et al. (2021; experiment 1 and 2) study using very different TBW tasks, suggests that task specific factors may be less important than other factors such as context.

Modulation of TBW and SoA window by occipital tACS.

In terms of the second aim of the current study, we found the occipital tACS stimulation at the upper bound of the alpha frequency range (14Hz), reduced the width of both the TBW and the SoA window, compared to stimulation at the lower bound of the alpha range (8Hz). These results support previous findings in the field (Cecere et al., 2015; Migliorati et al., 2020; Samaha & Postle, 2015), which have linked the alpha peak frequency to the width of the TBW. Moreover, the current study revealed novel evidence suggesting that alpha peak frequency is also related to the SoA window. As discussed earlier, this association might be explained by the observation that tACS has also been shown to influence time perception (Mioni et al., 2020), which in turn will feed into the time window of SoA.

However, it must be noted that as we did not employ a tACS condition at any other electrode locations (a control condition), it is not possible to rule out the possibility that the tACS modulation was not directly related to the occipital alpha cycle. For instance, stimulation of the peripheral nerves could cause tactile sensation, which in turn could then drive the effect of the stimulation as opposed to the frequency of the alpha peak. However, this possibility seems to be unlikely. Firstly, participants were actively encouraged to report any scalp tactile sensations not only during the set-up but throughout the experiment. A debriefing session confirmed that none of the participants experienced scalp tactile sensation once the experiment began. Hence, any tactile sensation would be below perceptual threshold and hence unlikely to induce the effect of the stimulation. It is worth noting that the previous studies in this field on which this research was based (Cecere et al., 2015; Mioni et al., 2020), also did not include any additional control montage. Nevertheless, to ensure that sub threshold tactile sensation is not interfering with the findings (in this and other studies), further research should add a control condition (using different montage i.e. stimulation excluding modulation of the frequency of the occipital alpha peak) to rule out more generalised effects of tACS simulation.

Conclusions

Firstly, the current study explored the relationship between the TBW and SoA. In contrast to Venskus et al. (2021; experiment 1 and 2), we did not find association between an individual's TBW and their SoA window. Nonetheless, we showed that both the TBW and the SoA window are modifiable via tACS stimulation of the upper versus lower bound of the frequency of the alpha peak. This provides novel evidence for a possible common neural mechanism linking the TBW and the time window of SoA, namely the frequency of the occipital alpha peak.

Chapter Four: The relationship between temporal sensitivity and sense of agency.

The study described in this chapter have been submitted to Consciousness and Cognition and is currently at the stage of Revisions Under Review.

Abstract

Sense of agency refers to the feeling of being in control of one's actions and their associated outcomes. One important aspect of a sense of agency seems to be the temporal grouping of sensory information. One previous study has shown that the time window of sense of agency is associated with individual differences in temporal sensitivity. The current study extends this knowledge by exploring how metacognition of agency in complex action-outcome relationship links to temporal sensitivity. Participants used a mouse to control a cursor along the bottom of the screen in order to either hit or avoid falling objects. The cursor either moved precisely in line with their movement, or with some delay (lag) or added movement (turbulence). We evaluated whether the impact of these manipulations on the metacognition of agency, correlated with individual differences in temporal sensitivity (assessed by measuring temporal binding window using double-flash illusion task). We observed an association only during long lag manipulations. Here, in contrast to our predictions, we found that increased sensitivity of metacognition of agency was associated with a less precise temporal sensitivity. This suggests that the relationship between temporal sensitivity and sense of agency observed in previous studies is less prevalent in more complex action-outcome relationships where metacognition of agency is involved, as here, a wider range of possible agency cues are present. That is, in the presence of other agency cues, metacognition of agency may depend more on these other cues than temporal sensitivity per se.

Keywords: Temporal Sensitivity, Metacognition of Agency, Temporal Binding, Double-flash Illusion, Multisensory Integration

Introduction

Sense of agency (SoA) refers to the feeling of being in control of one’s actions and their associated outcomes (i.e. the feeling of having caused a sensory event in the environment) (Buehner & Humphreys, 2009; Farrer et al., 2013; Moore & Fletcher, 2012; Moore & Haggard, 2008). One important aspect of SoA seems to be the temporal grouping of sensory information (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). More than three decades ago Shanks et al. (1989) showed that a reduction in SoA is observed when the interval between an action and an associated sensory outcome is increased. More recently, Kawabe et al. (2013) suggested that SoA seems to depend on temporal grouping of actions and outcomes. That is, when an action is accompanied with additional sensory event that event, rather than the outcome, is integrated with the action, consequently reducing SoA for an outcome. In addition, Farrer et al. (2013) proposed that if action and outcome occur within a specific temporal interval, within which the action and the outcome are integrated, one experiences a greater SoA. In their study, participants were required to perform an action (a button press) that elicited an outcome (appearance of a circle on a screen) with various delays and to report their sense of agency over that outcome. Findings indicated that participants were more likely to report SoA for the outcome at shorter delays as opposed to longer delays, supporting the notion that SoA depends on the temporal relationship between action and outcome.

In turn, temporal grouping of sensory information is dependent on the individual`s temporal sensitivity (the ability to detect a time-based discrepancy between two stimuli and consequently determining whether sensory information is grouped or not; Watson, 1986). One common way to assess temporal sensitivity is by exploring the width of the temporal binding window (TBW), within which incoming multisensory information is integrated (Cecere et al., 2015; Ferri, et al., 2018; Haß et al., 2017; Stevenson et al.,2014). The TBW is often measured using the double-flash illusion (Keil, 2020). In this task, an individual is presented with simultaneous visual (flash) and auditory (beep) stimuli followed by a second auditory (beep) stimulus presented at various delays. If the second auditory stimulus occur within the individual’s TBW not just the first auditory stimulus is integrated with the visual stimulus but also the second auditory stimulus. This creates an illusion whereby participants report experiencing two flashes despite the fact that only one flash is ever presented. The delay at which the individual no longer perceives two flashes is taken as the width of their TBW, and acts as an index of their temporal sensitivity (see Hirst et al., 2020; Keil, 2020 for recent reviews). Previous research has shown that the TBW correlates with various measures of temporal sensitivity (Stevenson et al., 2010; Stevenson et al., 2011; Stevenson & Wallace, 2013). For example, Stevenson and Wallace (2013) showed that judgements of multisensory integration (perceptual fusion illusion) showed high consistency with two different measures of temporal sensitivity (temporal order judgement, and simultaneity judgement), across a range of different sensory modalities. As such, although tasks such as the double-flash illusion do not directly ask participants to separate stimuli in time, they seem to assess the same underlying process more indirectly.

As the temporal grouping of sensory information is dependent on temporal sensitivity it is plausible that SoA is partly influenced by the differences in an individual’s temporal sensitivity. The link between temporal sensitivity and SoA is supported by recent evidence showing that less precise temporal sensitivity (wider TBW) is associated with a less precise SoA (wider window of SoA - time frame within which the signals related to the action and to its outcome are integrated; Venskus et al., 2021). In that study, TBW was measured using double-flash illusion task discussed previously and SoA was measured using an agency task adapted from Farrer et al. (2013). This task involved participants pressing a key on the keyboard which triggered a circle to appear on the screen after a variable delay. Participants judged if they were controlling the appearance of the circle, or if the computer was controlling the appearance of the circle. The length of the delay at which participants' belief of controlling the appearance of the circle declined was taken as their SoA window.

The above shows that SoA and temporal sensitivity are linked in a simple action-outcome task. The current study aimed to extend this knowledge by exploring how SoA and temporal sensitivity might interact in a more complex action-outcome task involving metacognition of agency. Existing literature contains some preliminary findings indicating that metacognition of agency is associated with the temporal aspects of the tasks. For example, Metcalfe and Greene (2007) used metacognition of agency task, which involves participants playing a space invaders type game requiring them to catch Xs and avoid Os as they descend down the screen while different manipulations are introduced. Over four experiments Metcalfe and Greene (2007) introduced either noise (turbulence) to the movement, various speed levels of the targets descending, a magic element where the target was caught if the cursor was close to the target, and/or auditory feedback where different sound was presented when target or non-target was caught. They found that performance (calculated using caught targets), metacognition of performance (self-rating of the performance) and metacognition of agency (control participants felt over the outcome) was dependent on the various manipulations. That is, performance decreased with increased turbulence and with faster moving targets, and increased in the magic condition, with the metacognition of performance mirroring the performance. More interestingly, metacognition of agency decreased with increased turbulence, faster moving targets and also in the magic condition. In other words, people seem sensitive to the manipulations and able to identify when they are/are not in control of the cursor. Moreover, these findings also suggest that metacognition of agency is affected by the temporal relationship between an action (in this case moving of the mouse) and an outcome (in this case movement of the cursor). That is, when there is large temporal discrepancy between an action and an outcome metacognition of agency is reduced. Moreover, metacognition of agency task seems to have been successfully used in previous studies to investigate differences in metacognition of agency in various populations (general population vs schizophrenia patients; Metcalfe et al., 2014, general population vs highly suggestible individuals; Terhune & Hedman, 2017). Hence, showing that metacognition of agency task seems to be an effective means by which to explore individual differences in metacognition of agency. As such, this task seems to be an effective means by which to explore whether metacognition of agency is associated with an individual`s temporal sensitivity.

In the current study, on each trial we manipulated either the lag between the participants action and the movement of the on-screen cursor, or we introduced noise (turbulence) to the movement or we altered the speed with which the targets descended. Based on findings from studies exploring metacognition of agency (Metcalfe et al., 2014; Metcalfe & Greene, 2007; Terhune & Hedman, 2017) and those of Venskus et al. (2021, chapter three of this thesis) we predicted that individuals with less precise temporal sensitivity (increased TBW measured using the double-flash illusion) would have reduced metacognition of agency (be less sensitive to the agency manipulations).

Method

Participants

The sample consisted of 42 participants (as previous studies have used similar sample sizes; Metcalfe & Greene, 2007; Venskus et al., 2021, chapter three of this thesis), who were student volunteers from the University of Essex recruited via the University research advertisement websites. All participants had normal or corrected to normal vision and hearing to avoid these variables influencing the tasks. The local ethics committee approved the study, and participants gave their informed consent before taking part in the study. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki and approved by the University of Essex`s Faculty Ethics Subcommittee (departmental reference no: AV1901). Data is made accessible on OSF via the following link: https://osf.io/vs5u7/?view_only=959a39b5b1b846409b64c70d52c0fa89.

Exclusion Criteria

All 42 participants completed the double-flash illusion task and metacognition of agency task. The data sets that did not fit the psychometric sigmoid function (R^2 less than .6) or were incomplete could not be used in the further analysis (8 data sets in double-flash illusion task and none in metacognition of agency task). Given TBW was included in an ANCOVA as a covariate, complete data sets needed to be used. Thus, the final sample consisted of 34 data sets.

Design

The metacognition of agency task followed a within-subjects design. Conditions consisted of speed (slow, fast), lag (short, long), turbulence (weak, strong) and control (slow and fast speed with no lag or turbulence) condition. Dependent variables were performance (hits; i.e. the number of targets touched), metacognition of performance (subjective experience of how well the targets were captured and non-targets avoided) and metacognition of agency (subjective experience of whether they were in control of the cursor, from no control to complete control). The double-flash illusion task involved 15 (inter-beep intervals) within-subjects conditions with the dependent variable being whether participants experienced one flash or two flashes.

Apparatus/Materials

<u>Double-flash illusion task</u>

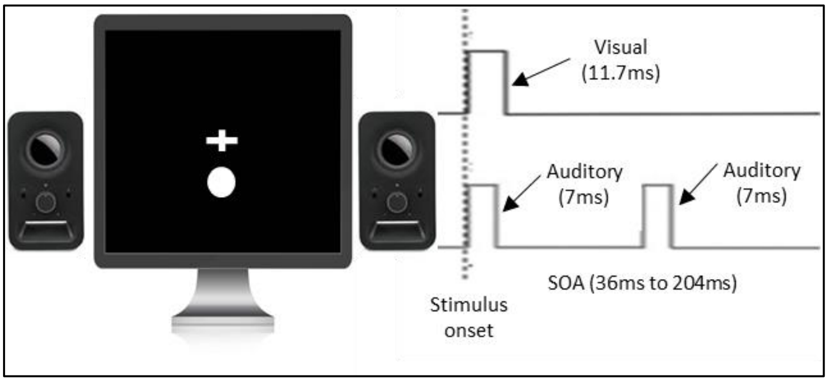

Figure 4.1: Paradigm of the double-flash illusion task.

The double-flash illusion task (see Figure 4.1) used was the same as that in the study of Cecere et al. (2015). E-Prime software (Psychology Software Tools, Pittsburgh, PA) and a 17 inch CRT monitor with a refresh rate of 85Hz (ViewSonic Graphics Series G90FB, refresh rate 85Hz) were used to present visual stimuli (flash). Visual stimuli were 11.7ms in duration and in the form of a white circle 1.32cm in diameter. Visual stimuli were located 1cm below the fixation cross that was positioned in the centre of the screen. Such characteristics of stimuli were chosen as it has been shown that tasks involving multisensory integration are optimised when visual stimuli are displayed in peripheral vision (Shams et al., 2002). Auditory stimuli were presented via two typical PC stereo speakers. In order to minimise the possible effect of the spatial cues on the perception of the task, speakers were placed at each side of the monitor and raised to align with the position of the visual stimuli (Macaluso et al., 2004). The auditory stimuli (beep) were presented for 7ms and consisted of a sinusoidal pure tone with a frequency of 3.5kHz and a sampling rate of 44.1kHz played at a constant volume. The above durations of the visual and auditory stimuli were chosen as they have previously been successfully employed to measure multisensory integration (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). The first auditory stimulus was aligned with the onset of the visual stimulus. The second auditory stimulus was presented in one of the possible inter-beep intervals. Inter-beep intervals ranged from 36ms to 204ms in 12ms steps. The above range of inter-beep intervals was chosen as numerous previous studies (such as Cecere et al., 2015;

Ferri et al., 2018) showed that such range not only captures but also extends beyond the time frame within which the double-flash illusion task is perceived. In terms of the inter-beep intervals being in 12ms steps, such interval was chosen as previous studies have shown that variations of width of the TBW can be even captured successfully with 25ms steps (Hab et al., 2017). We decided to use the smallest possible steps (monitor refresh rate being 85Hz) to ensure that even slight variations in TBW are captured. Each trial started with a white fixation cross in the centre of the monitor that remained on the screen throughout the trial. On each trial, visual and auditory stimuli were presented simultaneously, with the second auditory stimulus being presented in one of the possible inter-beep intervals randomly. Participants performed one block. Each inter-beep interval was presented 20 times, for a total 300 trials. Participants were instructed to always fixate on the fixation cross and report whether they perceived one or two flashes by pressing the key `1` or the key `2` respectively. Providing a response triggered the start of the next trial. The time interval between the beeps at which participants no longer stated they saw two flashes was calculated to be the width of their TBW.

Metacognition of agency task

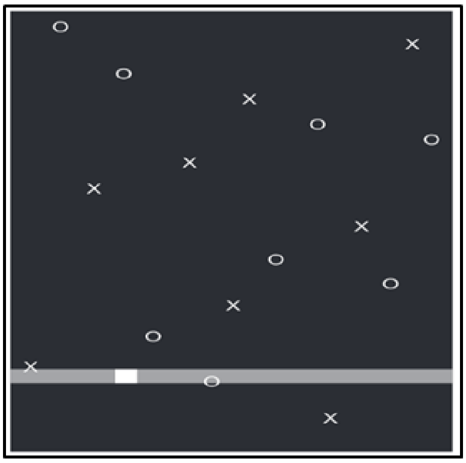

Figure 4.2: Example screenshot of the metacognition of agency task.

All stimuli were presented on the LCD monitor with a refresh rate of 60Hz using MATLAB running Psychtoolbox extension (Brainard, 1997) in a window of 864 x 1152 pixels. The task involved participants playing a game where Xs and Os descend from the top of the screen towards a horizontal line at the bottom of the screen (see Figure 4.2). To play the game participants were required to move the cursor along the horizontal line and catch as many Xs as possible while avoiding as many Os as possible. Cursor movement was only permitted on the horizontal plane, and as such any vertical mouse movements were ignored. On each trial we manipulated the speed of the stimuli, the lag of the cursor movement, and the amount of turbulence in the cursor movement. Manipulation of the speed of the stimuli involved 2 levels (i.e. slow speed, fast speed). The stimuli moved from the top of the screen to the bottom of the screen in steps of either 8 pixels per refresh (slow speed) or 10 pixels per refresh (fast speed). The stimuli refreshed on every second screen refresh (60Hz refresh rate; 16.6ms refresh time), giving a stimulus refresh time of 33ms. This meant that in slow speed condition (speed of 8 pixels per refresh), each stimulus took 4.8s to move from the top to the bottom of the screen, while in the fast speed condition (speed of 10 pixels per refresh), this was approximately 3.8s. Manipulation of lag involved 3 levels (i.e. no lag, short lag, fast lag). In the no lag condition the cursor started moving in time with the movement of the mouse, in the short lag condition the cursor started moving with a delay of 100ms, and in the long lag condition the cursor started moving with a delay of 200ms. Manipulation of turbulence involved 3 levels (i.e. no turbulence, weak turbulence, strong turbulence). In the no turbulence condition the displacement of the cursor moved with the displacement of the mouse. In the turbulence conditions, on each screen refresh the displacement of the cursor was distorted with respect to the movement of the mouse. The position of the cursor on each refresh was calculated by the actual mouse position plus an additional value. This additional value was 50% of the displacement from the last screen refresh in the strong turbulence condition and 25% of the movement in the weak turbulence condition. Importantly the cursor position was always the actual mouse position plus this distortion. As such, this distortion was not cumulative. If there was no movement on any given screen refresh, the cursor position was stable at the actual position of the mouse. This manipulation distorted the cursor movement in such a way that the jitter was less apparent during periods of movements of stable velocity, but became more apparent when participants slowed down, as they naturally would to position the cursor under a target. Similarly at the start of a movement, there would be a large jump ahead of the actual mouse position. This would make fine adjustments to the position of the cursor to align underneath a falling target more difficult. The task involved 60 trials lasting approximately 25s each. Each trial consisted of one of the possible conditions and was presented six times in random order. After each trial participants were instructed to rate their performance (metacognition of performance) on that trial and the control they felt over the cursor (metacognition of agency) on that trial. Rating was done using a visual continuous scale on the monitor. Providing a response triggered the start of the next trial.

Procedure

First participants had the opportunity to ask any questions and signed a consent form. Participants were then seated in a dimly lit room approximately 60cm away from the computer screen with the plane of their eyes aligned to the middle of the monitor. Participants completed the double-flash illusion task and the metacognition of agency task with the order of the tasks being counterbalanced. Before commencing the tasks, participants received detailed instructions and were given practice trials. Before commencing the double-flash illusion task participants were instructed to fixate on the fixation cross in the middle of the monitor for the duration of the trial. Participants were told that the flash will appear below the fixation cross and they need to report after each trial whether they perceived 1 or 2 flashes by pressing 1 or 2 on the keyboard. Before commencing the metacognition of agency task participants were instructed to use the cursor on a horizontal plane to capture as many Xs as possible while avoiding as many Os as possible. Participants were informed that they will have to rate their performance on that trial and the control they felt over the cursor on that trial. In terms of the performance rating participants were told to use the slider on the computer monitor. If none of the Xs were captured and all of the Os were captured, participants were told to press on the far left of the slider and vice versa. Additionally, participants were told that if their performance was not at the extreme ends they should click somewhere in-between to reflect their performance. In terms of the control felt over the cursor participants were instructed to also use a slider to indicate their response. If no control was felt participants were told to click of the far left of the slider and vice versa. Additionally, participants were told that if their feeling of control was not at the extreme ends they should click somewhere in-between to reflect their feeling of control.

Data Analysis

To assess the width of the TBW, the time window in which the illusion was maximally perceived, the percentage of trials where two flashes were reported was first plotted as a function of the inter-beep delay. A psychometric sigmoid function was then fitted to the data. The sigmoid function was defined by the equation: $y = a+b/(1+exp(-(x-c)/d))$ (a = upper asymptote; b = lower asymptote; c = inflection point; d = slope). For each participant, c was taken as the TBW, i.e. the point of decay of the illusion (Cecere et al., 2015). In the metacognition of agency task we first analyzed how performance (calculated by determining how many Xs out of all possible (27) were captured), metacognition of performance (calculated by converting to percentage the provided location on the visual analogue continuous scale) and metacognition of agency (calculated by converting to percentage the provided location on the visual continuous analogue scale) varied as a function of speed, lag, and turbulence. In line with previous studies, (Metcalfe et al., 2014; Metcalfe & Greene, 2007; Terhune & Hedman, 2017). We measured performance using the number of captured targets. Moreover, we calculated dPrime scores (overall performance including hitting non-targets) and found the same pattern as that of scores based on captured targets only. (Data is made accessible on OSF via the following link: https://osf.io/vs5u7/?view_only=959a39b5b1b846409b64c70d52c0fa89.) Also, since the lag and turbulence manipulation did not each have independent control conditions (no lag was the same as no turbulence) we performed separate ANOVAs for lag and turbulence with no lag and no turbulence condition being the control condition for both variables. In each case a repeated measures ANOVA was conducted with 2 factors, speed (slow, fast) and turbulence/lag (control, weak, strong/control, short, long). Greenhouse-Geiser corrections were applied where sphericity assumptions were violated.

To investigate the link between the individual differences in SoA and TBW we included participants mean-centered TBW as a covariate in the analysis. To further explore this, we correlated the width of the TBW with the contrast scores of lag and turbulence separately for the slow and fast speeds. Contrast scores were calculated by the following formula with C referring to control condition and E referring to one of the experimental conditions (short lag, long lag, weak turbulence, strong turbulence). Contrast score = (metacognition of performance C– metacognition of agency C) – (metacognition of performance E– metacognition of agency E). This contrast score is designed to test the degree to which participants attribute their drop in performance to be entirely under their control. A negative score means that the particular manipulation had a greater impact on their metacognition of performance than it did on their metacognition of awareness. In other words, they were aware that they were not entirely in control of their performance. Previous studies using the metacognition of agency task have shown that this score is typically negative in young adults, but decreased across the lifespan (Metcalfe et al., 2010), and is near zero in patients with schizophrenia (Metcalfe et al., 2014). As such this measure has previously been successfully employed to study individual differences in metacognition of agency.

Results

Descriptive Statistics

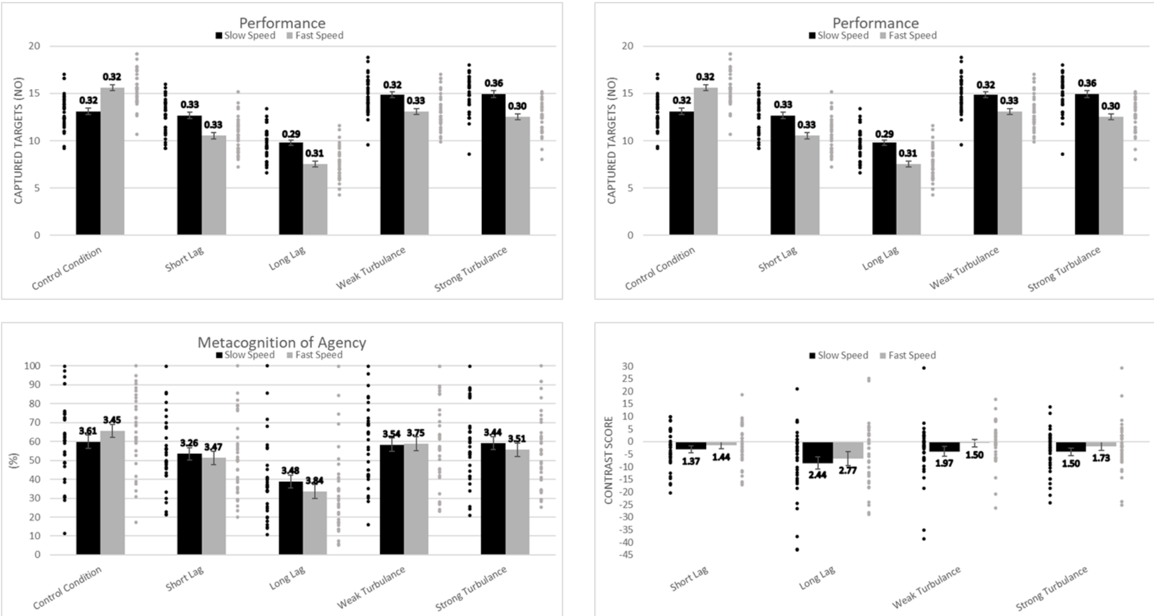

Figure 4.3: Performance (calculated by determining how many Xs out of all possible (27) were captured), metacognition of performance (calculated by converting to percentage the provided location on the visual analogue scale) and metacognition of agency (calculated by converting to percentage the provided location on the visual analogue scale) varied as a function of speed, lag, and turbulence. Contrast scores in the lag and turbulence conditions at slow and fast speed. A negative contrast score indicates that an individual has awareness of their control being disrupted by the manipulation. A contrast score of zero indicates that an individual has no awareness of their control being disrupted by the manipulation (over and above the effect of metacognition of performance). Dots represent individual data points. Error bars represent the standard error of the mean (SEM).

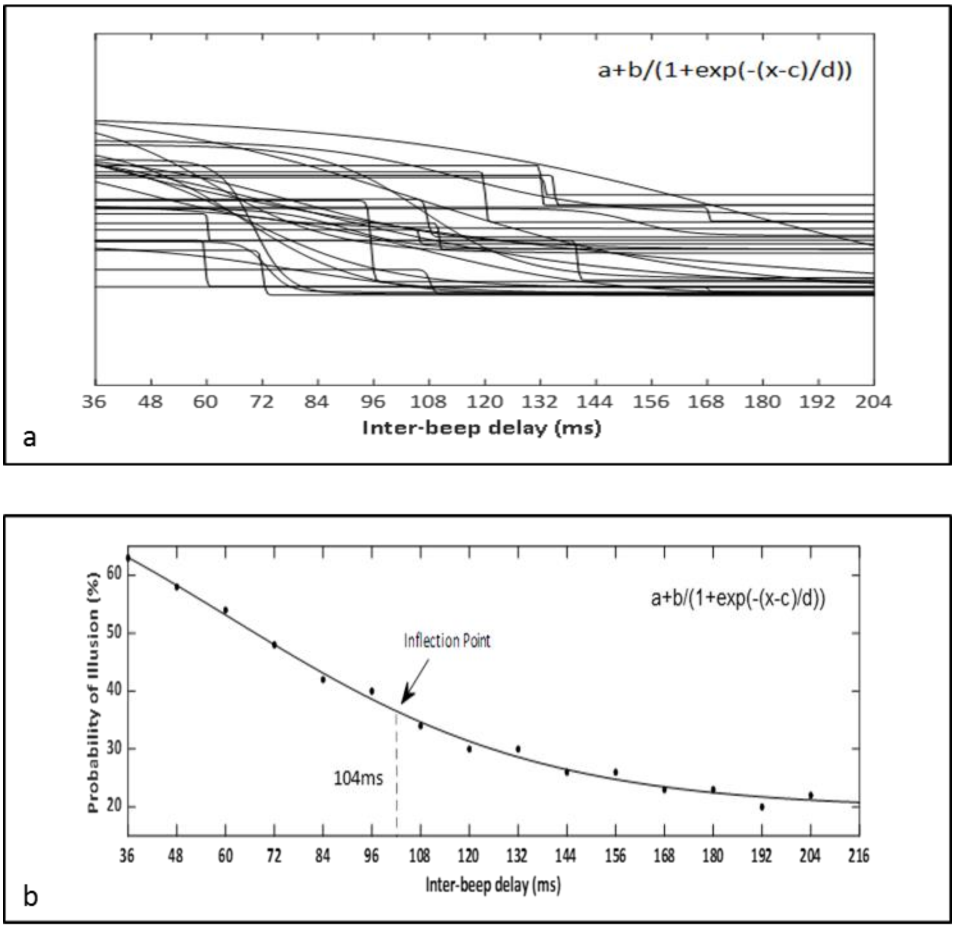

Figure 4.4: (*a) Percentage of probability of perceiving the illusion plotted as a function of inter-beep delay for each data set. A sigmoid function was then fitted to each data set`s data points. The black solid curve represents the sigmoid fit determining the point of decay of the illusion. (b) Average percentage of probability of perceiving the illusion plotted as a function of inter-beep delay. A sigmoid function was then fitted to the averaged data points. The black solid curve represents the sigmoid fit determining the point of decay of the illusion (104ms), corresponding to the width of the TBW. The points represent across-participants average raw data.*

Lag Analysis

Repeated measures ANCOVAs with the Bonferroni correction were used to analyse the data (alpha level=.008). Performance (see Figure 4.3) was significantly influenced by lag, $F(2,64)=364.61, p<.001$, , $\eta_p^2=.919$, speed, $F(1,32)=17.58, p<.001$, $\eta_p^2=.355$, and their interaction, $F(2,64)=133.77, p<.001$, $\eta_p^2=.807$. None of these factors interacted with TBW, (lag: $F(2,64)=0.47, p=.626$, $\eta_p^2=.015$, speed: $F(1,32)=0.01, p=.940$), $\eta_p^2<.001$, suggesting that individual differences in temporal sensitivity did not influence task performance. In terms of metacognition of performance (see Figure 4.3), we observed significant main effects of lag, $F(1.476,47.235)=91.11, p<.001$, $\eta_p^2=.740$, as well as a significant interaction between lag and speed, $F(2,64)=19.59, p<.001$, $\eta_p^2=.380$, but main effect of speed was non-significant, $F(1,32)=5.30, p=.028$, $\eta_p^2=.142$. Once again, none of these effects were seen to interact with TBW, (lag: $F(2,64)=0.17, p=.844$, $\eta_p^2=.005$, speed: $F(1,32)=0.43, p=.517$, $\eta_p^2=.013$). Metacognition of agency (see Figure 4.3) varied significantly as a function of lag, $F(1.332,42.610)=83.54, p<.001$, $\eta_p^2=.723$, as well as the interaction between lag and speed, $F(2,64)=10.90, p<.001$, $\eta_p^2=.254$, but not as a function of speed, $F(1,32)=0.72, p=.403$, $\eta_p^2=.022$. As previously, there was a non-significant interaction between these effects and TBW, (lag: $F(2,64)=3.62, p=.033$, $\eta_p^2=.101$, speed: $F(1,32)=2.01, p=.159$, $\eta_p^2=.061$). A sensitivity power analysis showed that our sample size had 80% power to detect medium effect sizes for two-way ANCOVA ($f = 0.64$; $\alpha = 0.008$, two-tailed).

Turbulence Analysis

Repeated measures ANCOVAs with the Bonferroni correction were used to analyse the data (alpha level=.008). Performance (see Figure 4.3) was significantly influenced by turbulence, $F(2,64)=8.75, p<.001$, $\eta_p^2=.215$, speed, $F(1,32)=25.85, p<.001$, $\eta_p^2=.447$, and their interaction, $F(2,64)=131.58, p<.001$, $\eta_p^2=.804$. None of these effects interacted with TBW, (turbulence: $F(2,64)=1.31, p=.278$, $\eta_p^2=.039$, speed: $F(1,32)=1.15, p=.291$, $\eta_p^2=.035$). Metacognition of performance (see Figure 4.3) was significantly affected by the interaction between turbulence and speed, $F(2,64)=18.10, p<.001$, $\eta_p^2=.361$, but not speed, $F(1,32)=2.12, p=.155$, $\eta_p^2=.062$, or turbulence, $F(1.633,52.246)=4.60, p=.014$, $\eta_p^2=.126$. Once again none of these factors interacted with TBW, (turbulence: $F(2,64)=0.94, p=.398$,

η_p^2=.028, speed: *F(1,32)=0.01,p=.907*, η_p^2<.001). Metacognition of agency (see Figure 4.3) was significantly influenced by turbulence, *F(2,64)=10.21,p<.001*, η_p^2=.242, as well as the interaction between turbulence and speed, *F(2,64)=7.92,p<.001*, η_p^2=.198, but not speed, *F(1,32)=1.77,p=.193*, η_p^2=.052. Similarly to above, none of these factors interacted with TBW, (turbulence: *F(2,64)=2.50,p=.090*, η_p^2=.073, speed: *F(1,32)=0.30,p=.590*, η_p^2=.009). A sensitivity power analysis showed that our sample size had 80% power to detect medium effect sizes for two-way ANCOVA (f = 0.64; α = 0.008, two-tailed).

Relationship between Metacognition of Agency and Temporal Sensitivity

To investigate in more detail the relationship between individual differences in metacognition of agency and temporal sensitivity we correlated turbulence and lag contrast scores (see Figure 4.3) with the TBW (see Figure 4.4). This revealed non-significant relationship between TBW (α = 0.98) and weak turbulence (α = 0.99) at slow speed, *r(32)=-0.26,p=.139*, Bayes Factor=2.54 (null versus alternative), as well as between TBW (α = 0.98) and weak turbulence (α = 0.99) at fast speed, *r(32)=-0.26,p=.144*, Bayes Factor=3.13 (null versus alternative). Non-significant relationship was also revealed between TBW (α = 0.98) and strong turbulence (α = 0.99) at slow speed, *r(32)=-0.23,p=.184*, Bayes Factor=2.60 (null versus alternative), as well as between TBW (α = 0.98) and strong turbulence (α = 0.99) at fast speed, *r(32)=-0.23,p=.187*, Bayes Factor=3.17 (null versus alternative). Similarly, a non-significant relationship between TBW (α = 0.98) and short lag (α = 0.99) at slow speed, *r(32)=-0.13,p=.465*, Bayes Factor=5.76 (null versus alternative), as well as between TBW (α = 0.98) and short lag (α = 0.99) at fast speed, *r(32)=-0.16,p=.355*, Bayes Factor=4.91 (null versus alternative), was obtained. However, a significant moderate negative relationship between TBW (α = 0.98) and long lag (α = 0.99) at slow speed, *r(32)=-0.36,p=.039*, Bayes Factor=0.91 (null versus alternative), as well as between TBW and long lag (α = 0.99) at fast speed, *r(32)=-0.41,p=.017*, Bayes Factor=0.44 (null versus alternative), was observed (see

Figure 4.5). Thus, indicating that as the width of the TBW increases (reduced temporal sensitivity) metacognition of agency increases (A negative contrast score means that the participants feel more loss of control of their reduced performance). That is, as the width of the TBW increases lag has more of an influence on the participants` metacognition of agency. A sensitivity power analysis demonstrated that our sample had 80% power to detect moderate correlation of 0.46 or greater (α=.05, two-tailed).

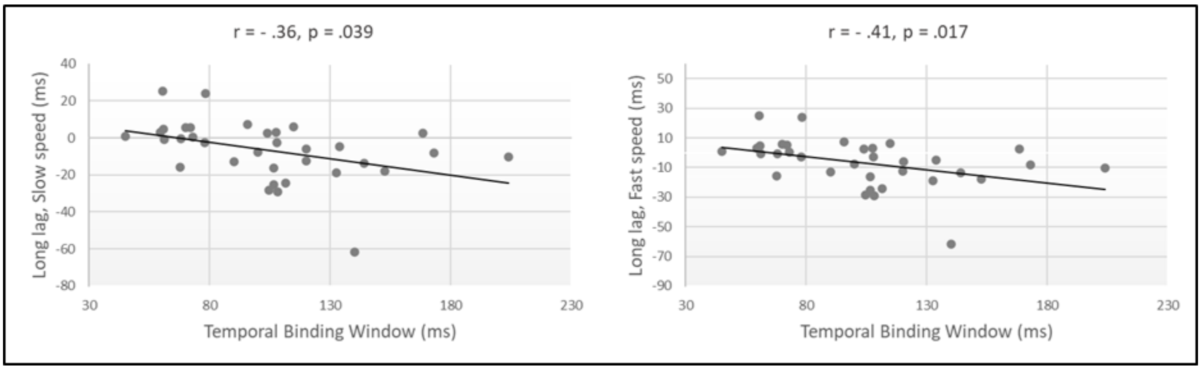

Figure 4.5: Scatterplot showing relationship between the temporal binding window and the long lag at slow/fast speed. Temporal binging window increases lag has less of an influence on the participants` metacognition of agency.

Discussion

Based on previous research showing that temporal sensitivity is associated with SoA in the case of a simple action-outcome relationship (Venskus et al., 2021, chapter three of this thesis), the current study aimed to investigate to what degree, if any, temporal sensitivity and SoA are related in more complex action-outcome relationship where metacognition of agency is involved. Given previous literature, it was predicted that less precise temporal sensitivity would be associated with reduced metacognition of agency. We found an association only during long lag manipulations. Here, in contrast to our predictions, we observed that increased sensitivity of metacognition of agency was associated with a less precise temporal sensitivity.

One possible explanation for the lack of an association between metacognition of agency and temporal sensitivity, might be because SoA is considered a higher-cognitive process (Frith & Dolan, 1996). Experiencing SoA involves various mental activities being executed simultaneously, voluntary and with controlled awareness (Moore & Fletcher, 2012; Moore et al., 2009; Synofzik et al., 2008; Synofzik et al., 2013). More specifically, existing literature has shown SoA to be modulated by many different cues in addition to temporal cues (Chambon et al., 2014; Moore & Fletcher, 2012). For example, action selection fluency is thought to be involved (Chambon et al., 2014; Wenke et al., 2010) as well as the consistency between the predicted and the actual outcome affects SoA. The former refers to a notion that SoA is influenced by the action selection in advance of the action itself, and before action outcomes are known (Chambon & Haggard, 2012). The latter can be explained in terms of predictive processes (Frith et al., 2000), postdictive confabulation (Wegner, 2002) as well as integration of prior information about a similar task (Moore & Fletcher, 2012).

With this in mind, we should consider how these different cues might relate to the metacognition of agency task used in the current study, as compared to the more basic agency task used in Venskus et al. (2021, chapter three of this thesis) study. In the metacognition of agency task, participants played a game where Xs and Os descend from the top of the screen towards a horizontal line at the bottom of the screen. To play the game participants were required to move the cursor along the horizontal line and catch as many Xs as possible while avoiding as many Os as possible. Bearing in mind the characteristics of the task, participants needed to make a conscious decision to move the cursor to a specific location to capture Xs and/or avoid Os. As previously mentioned, according to action selection fluency (Chambon et al., 2014; Wenke et al., 2010) selecting what action to perform might generate a SoA. As such, it could be that action selection fluency contributed to the experience of SoA, as moving the cursor on the manipulated trials might have felt less fluent. It is also likely that the comparison between the predicted and the actual outcome (Frith et al., 2000; Moore & Fletcher, 2012; Wegner, 2002) plays a role in the experience of SoA in the task. More specifically, it is reasonable to assume that participants predicted that the cursor would move to the intended location due to their previous experiences involving cursor movements. Hence, such expectations might have triggered experience of SoA, even if the cursor movement was somewhat delayed. Given the above, temporal sensitivity may have played a relatively minor part in the experience of SoA in metacognition of agency task and instead other cues may have had a stronger influence. In contrast, in Venskus et al. (2021, chapter three of this thesis), time was the only cue available to inform SoA. In particular, the task involved participants judging whether their key press triggered the appearance of the circle or if the computer was controlling the appearance of the circle. As participants only had to press the key and await the appearance of the circle, they did not have cues such as action selection fluency or consistency between the predicted and actual outcome cues available to them, with the only cue being the temporal relationship. Hence it seems to be reasonable to assume that temporal sensitivity and SoA should be related in such a task.

As discussed above, there are good reasons to assume why SoA is less dependent on temporal cues in the metacognition of agency task. However, our findings pointed towards the possibility that increased temporal sensitivity is associated with a reduced effect of the task manipulations of metacognition of agency. One possible explanation for this finding could be that the individual`s precision of temporal sensitivity influences the degree to which they rely on different agency cues. It might be possible that people with a less precise temporal sensitivity stop using the temporal information as a cue and instead rely on other available cues more readily than people with more precise temporal sensitivity, which might actually have resulted in increased sensitivity of metacognition of agency. For instance, as lag increases performance reduces, thus the longer the lag the stronger the discrepancy between the predicted and the actual outcome consistency (Frith et al., 2000; Moore & Fletcher, 2012; Wegner, 2002). In this case, this might act as an even stronger agency cue than a temporal information cue. Thus, as participants with less precise temporal sensitivity pay more attention to the predicted cue and the actual outcome consistency cue than to temporal information cue, they are more sensitive to the lag. While this explanation is speculative, and it is also possible that the surprise reverse correlation we observed may not be genuine, the current study does appear to show that the relationship between temporal sensitivity and SoA observed in previous studies (Venskus et al, 2021, chapter three of this thesis), is less prevalent in a task that involves more complex action-outcome relationships and a wider range of possible agency cues.

Chapter Five: Perceptual training modifies temporal binding window and sense of agency but not alpha oscillations.

The study described in this chapter is in the final stages of preparation in order to be submitted to Brain and Cognition.

Abstract

Perceptual training has been argued to be a potential means via which to modify temporal sensitivity (the ability to detect time-based discrepancy between two stimuli) with previous studies providing preliminary evidence that perceptual training can lead to a change in the temporal binding window. Although temporal sensitivity has been suggested an important aspect of sense of agency, the effects of perceptual training on sense of agency have not been explored. Similarly, the effects of perceptual training on the proposed neural mechanism of temporal sensitivity (frequency of the EEG alpha peak) have also not been investigated. Therefore, the aim of this study was to explore the effects of perceptual training on sense of agency and the frequency of the alpha peak, as well as replicate previously observed effects on temporal binding window. Given the existing literature, it was predicted that the width of the sense of agency window, as with the width of the temporal binding window, will be reduced following perceptual training whereas the frequency of the occipital alpha peak will be increased. In line with predictions, the sense of agency window and temporal binding window were reduced after perceptual training. However, the frequency of the occipital alpha peak did not change. These findings present novel evidence indicating that perceptual training enhances sense of agency. Moreover, we argue that such cognitive changes perhaps are not permanent if not established within neural system. In terms of the frequency of the alpha peak staying unchanged, we explain these findings in terms of characteristics of our study.

Keywords: Perceptual Training, Temporal Sensitivity, Temporal Binding Window, Occipital Alpha Peak Frequency, Sense of Agency

Introduction

Temporal grouping of sensory information is subject to an individual's temporal sensitivity; that is, the ability to recognise a discrepancy in time between the instances of two stimuli (Colonius & Diederich, 2004). Existing research (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017; Stevenson et al., 2014) shows that temporal sensitivity varies significantly between individuals. Recent literature reviews (Hirst et al., 2020; Keil, 2020) have demonstrated that temporal sensitivity can be examined by measuring the temporal binding window (TBW). The TBW is defined as the window within which integration of incoming multisensory information takes place. The most common way to measure the TBW is through the use of a double-flash illusion task (Hirst et al., 2020; Keil, 2020). In this task an individual is presented with the simultaneous occurrence of a visual (flash) stimulus and an auditory (beep) stimulus. Following a variable delay, a second auditory (beep) stimulus is presented. When both beeps are within the individual's TBW, the flash is integrated with both beeps. This then results in the illusory of perception of a second flash. As such, the delay at which an individual no longer perceives two flashes is taken as the width of their TBW and acts as an index of their temporal sensitivity.

Recently it has been argued that an individual's alpha peak frequency might be the neural mechanism of the temporal sensitivity (Gibbon et al., 1984; Glicksohn et al., 2009; Horr et al., 2016; Luft & Bhattacharya, 2015; Mioni et al., 2020; Treisman, 1963; Treisman, 2013; Venskus et al., 2021, chapter three in this thesis; Wittmann & Van Wassenhove, 2009; Wittmann et al., 2010). Alpha oscillations are observable over posterior areas of the brain via electroencephalography (EEG) (Calomeni et al., 2017). Generally, the amplitude of oscillations in the brain decrease as the frequency increases. However, a clear peak is observed around 10 Hz (see Donoghue et al., 2020 for a comprehensive review). This peak is known as the occipital alpha peak. Typically, these oscillations range from 8Hz to 12Hz, but can be as low as 7Hz or as high as 14Hz (Mioni et al., 2020; Zhang et al., 2019). Higher temporal sensitivity has been associated with an increased frequency of the occipital alpha peak (Kononowicz & Van Wassenhove, 2016; Samaha & Postle, 2015). Given that higher temporal sensitivity results in shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews), a clear link between alpha peak frequency and the TBW emerges. This suggestion is supported by recent studies. For example, individual differences in the frequency of the alpha peak have been found to correlate negatively with the width of the TBW (Cecere et al., 2015; Migliorati et al., 2020; Venskus & Hughes, 2021, chapter two in this thesis). Furthermore, neuromodulation (via tACS) of the frequency of the occipital alpha peak alters the width of the TBW accordingly (increased frequency of the occipital alpha peak is associated with decreased width of the TBW; Cecere et al., 2015, Venskus et al., 2021, chapter three in this thesis).

In addition, sense of agency (SoA), the feeling of having caused a sensory event, appears to be influenced by temporal sensitivity (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). Experience of SoA is reduced when there is an increase in the interval between an action and a resulting sensory outcome (Shanks et al., 1989). This relationship seems to depend on temporal grouping of actions and outcomes (Kawabe et al., 2013). Moreover, Farrer et al. (2013) hypothesised that an individual experiences a greater SoA when an action and integrated outcome occur within a specific temporal interval. Their study required participants to press a button (action) that caused the appearance of a circle on a screen (outcome) over numerous occasions with various time delays. Participants were then required to report their SoA over the outcome. The results indicated that individuals felt greater SoA for the outcome where the delay was shorter and vice versa. Consequently, this supports the notion that SoA depends on the temporal relationship between action and outcome and therefore temporal sensitivity.

Furthermore, SoA appears to be associated with the neural mechanism of temporal sensitivity. This notion stems from the association of the time perception with the TBW (Fenner et al., 2020) and the alpha oscillations (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020). Additionally, time perception has been closely linked to SoA as the experience of SoA depends on the time interval between action and outcome (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). Given that SoA is associated with time perception, which in turn is associated with alpha oscillations, it seems likely that SoA might relate to peak alpha frequency. Indeed, a recent study by Venskus et al. (2021; chapter three in this thesis) showed that tACS stimulation over occipital electrodes at the higher and lower limits of the alpha range, modulates the width of the SoA window.

Recently, temporal sensitivity has been shown to be modifiable via perceptual training by shifting the point of subjective simultaneity (PSS), the discrepancy at which two stimuli are perceived as simultaneous, towards the optimum (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019). More precisely, the width of the TBW was shown to be reduced following perceptual training. Perceptual training involves judging stimuli as simultaneous or non-simultaneous with performance-based feedback being provided. If temporal sensitivity is related to SoA, one could hypothesise that enhancing temporal sensitivity via perceptual training would respectively modify SoA. As temporal sensitivity has been shown to similarly influence both TBW and SoA (Venskus et al., 2021; chapter three in this thesis) a decrease in the width of the SoA window, similarly to a decrease in the width of the TBW, following perceptual training seems to be likely. Moreover, it is also reasonable to speculate that if perceptual training affects temporal sensitivity, its neural mechanism (frequency of the occipital alpha peak) should also be affected. Given that previous findings indicate that increased frequency of the alpha peak is associated with the decrease of the width of the TBW (Gibbon et al., 1984; Glicksohn et al., 2009; Horr et al., 2016; Luft & Bhattacharya, 2015; Mioni et al., 2020; Treisman, 1963; Treisman, 2013; Wittmann & Van Wassenhove, 2009; Wittmann et al., 2010), the frequency of the alpha peak should be increased following the perceptual training.

Experiment 1 (Laboratory Setting)

Method

Participants

Initially, the study was designed to take place in a laboratory setting and preregistered with a sample of 65 participants, but had to be stopped with sample of 14 due to Covid-19 circumstances. The sample consisted of student volunteers from the University of Essex, recruited via the University research advertisement websites (i.e. SONA) with course credits as reimbursement. All participants had normal or corrected to normal vision and hearing to avoid these variables influencing the tasks. Participants gave their informed consent before taking part in the study. The study was approved by the local ethics committee and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki and approved by the University of Essex`s Faculty Ethics Subcommittee (departmental reference no: ETH1819-0211). Data is made accessible on a public repository - OSF via the following link: https://osf.io/u4x8v/?view_only=7802a3d16c8d4ad19044996769b704fa.

Data Exclusion

The data sets that did not fit the psychometric sigmoid function (R^2 less than .6) or/and contained incomplete data were removed from further analysis of double-flash illusion (5 data sets were removed) and judgement of agency task (3 data sets were removed). No data sets were removed from the EEG analysis.

Design

The current study used within-subjects design. The independent variable in the study was perceptual training with 2 conditions (pre perceptual training and post perceptual training). Dependent variables were the width of the TBW, the width of the SoA window and the frequency of the occipital alpha peak measured at both conditions.

Apparatus/Materials

Electroencephalography (EEG) recording

To measure the frequency of the occipital alpha peak continuous EEG was recorded from posterior sintered Ag/AgCI electrodes (Oz, O1, O2, PO3, POZ and PO4 channels) mounted on an elastic cap (EasyCap) using a Brain Products BrainAmp DC system for two minutes at rest with eyes closed. Left mastoid was used as a reference during recording. Data from a cluster of posterior electrodes was used as this was the only region of interest due to the frequency of the occipital alpha peak being at the maximum in this area (Cecere et al., 2015).

Perceptual Training

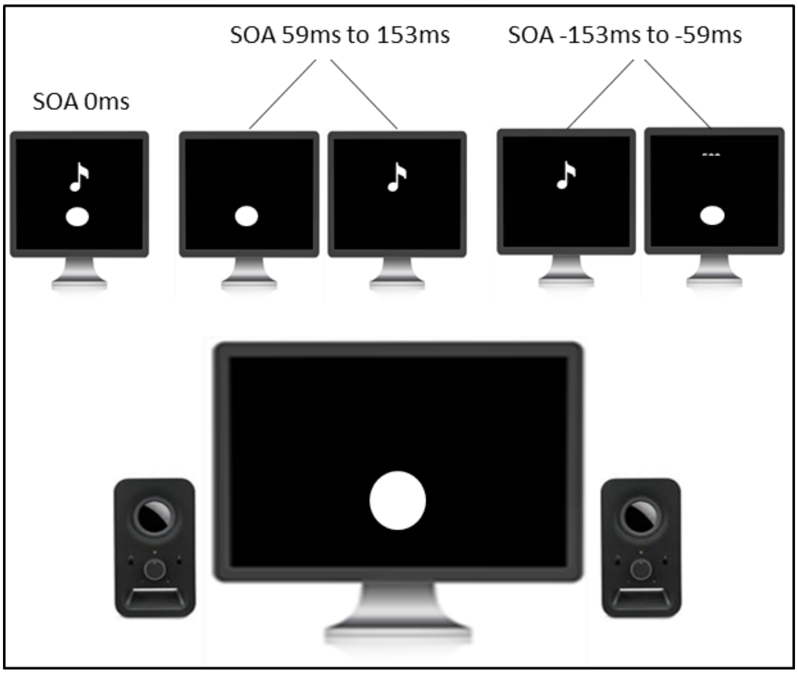

Figure 5.1: Paradigm of the perceptual training.

Perceptual training essentially is simultaneity judgement task with feedback (see Figure 5.1). All stimuli were presented on a CRT monitor with a refresh rate of 85 Hz using E-Prime (Psychology Software Tools, Pittsburgh, PA). Visual stimuli were 11.7ms in duration and auditory stimuli were 7ms in duration. Visual stimuli were in the form of a white circle with a diameter 1.32cm located 1 cm below the fixation cross that was positioned in the centre of the screen. This stimulus setup was chosen as it has been shown that tasks involving multisensory integration are optimised when visual stimuli are displayed in peripheral vision (Shams et al., 2002). Auditory stimuli were in a form of a 3500Hz pure tone presented via two typical PC stereo speakers. In order to minimise the possibility that spatial cues may affect the perception of the task, speakers were placed at each side of the monitor and raised to align with the position of the visual stimuli (Macaluso et al., 2004). The visual and auditory stimuli had stimulus onset asynchronies (SOAs) of either 0ms or 59ms, 106ms and 153ms (visual stimulus leading) or -59ms, -106ms and -153ms (auditory stimulus leading). SOAs were presented randomly and not equally distributed (the veridical simultaneous condition had a 6:1 ratio to any of the other 6 non-simultaneous conditions). In this way there was a random and equal likelihood of simultaneous/non-simultaneous conditions, minimizing concerns about response bias. Each trial started with the following instructions: “Please judge whether the flash and the beep are presented together or separate. Press `1` for together and `2` for separate. Once you have made the response feedback will be presented. Use this feedback to become better at determining whether the flash and the beep occur together or separate. Press any key to begin.” Thereafter participants were presented with the white fixation cross displayed in the centre of the monitor for 500ms. Once the fixation cross disappeared either visual stimulus, auditory stimulus or both stimuli together were presented. After presentation of the stimuli the following reminder message appeared: “Press `1` for together. Press `2` for separate.” and was displayed until response was made. Once the response was made participants were presented with either the phrase `Correct`, in green, or `Incorrect`, in red, for 1500ms. Thereafter next trial began. The task consisted of 900 trials with participant being able to take breaks when required.

Double-flash illusion (measure of TBW)

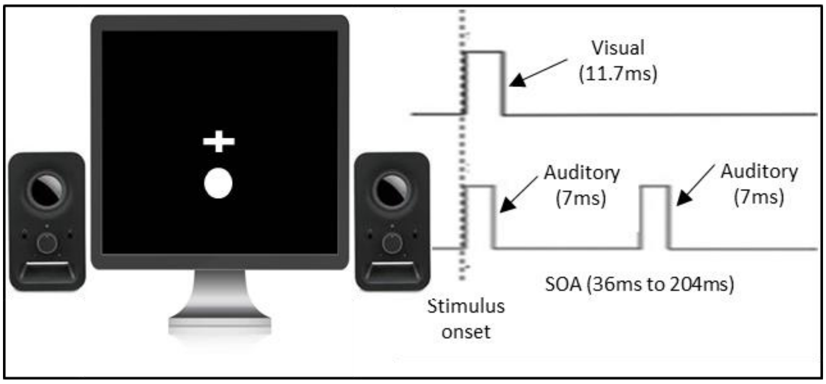

Figure 5.2: Paradigm of the double-flash illusion.

The double-flash illusion used was the same as that in the study of Cecere et al. (2015) (see Figure 5.2). We chose to use this version of the task, as it has previously been associated with individual differences in the EEG alpha peak frequency been successfully modulated by tACS (Cecere et al., 2015). All stimuli were presented on a CRT monitor with a refresh rate of 85 Hz using E-Prime (Psychology Software Tools, Pittsburgh, PA). Visual stimuli were 11.7ms in duration and auditory stimuli were 7ms in duration. Visual stimuli were in the form of a white circle with a diameter 1.32cm located 1 cm below the fixation cross that was positioned in the centre of the screen. This stimulus setup was chosen as it has been shown that tasks involving multisensory integration are optimised when visual stimuli are displayed in peripheral vision (Shams et al., 2002). Auditory stimuli were in a form of a 3500Hz pure tone presented via two typical PC stereo speakers. In order to minimise the possible effect of the spatial cues on the perception of the task, speakers were placed at each side of the monitor and raised to align with the position of the visual stimuli (Macaluso et al., 2004). Each trial started with a white fixation cross in the centre of the monitor that remained on the screen throughout the trial. On each trial, visual and auditory stimuli were presented simultaneously, and after a variable Stimulus Onset Asynchrony (randomly chosen between 36ms to 204ms in 12ms steps) a second auditory stimulus was presented. Participants performed one block. Each Stimulus Onset Asynchrony was presented 20 times, for a total 300 trials. Participants were instructed to fixate on the fixation cross and report whether they perceived one or two flashes by pressing the key `1` or the key `2` respectively. Judgement of agency (measure of SoA)

Figure 5.3: Paradigm of the judgement of agency task.

The judgement of agency task was adapted from Farrer et al. (2013) (see Figure 5.3). All stimuli were presented using MATLAB running Psychtoolbox extension (Brainard, 1997; Kleiner et al., 2007) on an LCD monitor with a refresh rate of 60Hz. Each trial started with a white fixation cross in the centre of the monitor. After a delay of 500ms the fixation cross disappeared, signalling the beginning of the trial. After the cross disappeared, participants were asked to press the space bar on the computer keyboard whenever they wanted. Once participants pressed the key, a circle of 2.5cm in diameter was displayed in the centre of the screen for 500ms with 11 possible delays ranging from 0ms to 1400ms in steps of 140ms. The task consisted of 2 blocks with each delay being presented 10 times in random order. In total participants completed 220 trials. Participants were required to judge if the appearance of the circle was caused by their button press, or if the computer had triggered the circle to appear. Participants were told that on some trials the computer would cancel their button press and re-trigger the appearance of the circle at a random interval. Participants needed to press key `1` if they thought that it was most likely they triggered the circle to appear and `2` if they thought that it was most likely computer triggered the circle to appear. This response approach was chosen over that of that of Farrer et al. (2013), where participants were given three choices (i.e. full control, partial control and no control), to avoid participants opting for the partial control if not fully sure. Such partial control responses would complicate the calculation of the time window of SoA, via the fitting of a sigmoid function.

<u>Procedure</u>

The study took place over 4 consecutive days. Day 1 – EEG data was recorded. Thereafter participants were seated in a dimly lit room approximately 60cm away from the computer screen with the plane of their eyes aligned to the centre of the monitor and double-flash illusion task as well as judgement of agency task completed. Day 2 and 3 - Participants were seated in a dimly lit room approximately 60cm away from the computer screen with the plane of their eyes aligned to the centre of the monitor. Participants then completed perceptual training. Day 4 – Replication of Day 1.

<u>Data Analysis</u>

To assess alpha peak frequency for eyes closed resting data, the 120 second periods were divided into epochs of one second. Bad channels and were removed by visual inspection. Noisy epochs were excluded using automatic artifact rejection in eeglab (Delorme & Makeig, 2004), with the joint probability parameter and kurtosis parameter set to 5, and amplitude threshold set to 5000. Each one second window was then multiplied by a Hanning taper, and zero-padded to 10 seconds. Power was computed from 4Hz to 30Hz using a fast Fourier transform (FFT function in matlab). The resulting FFT had a frequency resolution of 0.1Hz. The power at each frequency was normalising by subtracting the mean power across the spectrum, and dividing by the standard deviation. Based on previous studies and our finding of maximum power between 8Hz and 14Hz, we extracted the alpha peak frequency averaged across 6 posterior electrodes (Oz, O1, O2, PO3, POZ and PO4) at eyes closed at rest.

To assess the width of the TBW, the time window in which the illusion was maximally perceived, the percentage of trials where two flashes were reported was first plotted as a function of the inter-beep delay. A psychometric sigmoid function was then fitted to the data. The sigmoid function was defined by the equation: $y = a+b/(1+exp(-(x-c)/d))$ (a = upper asymptote; b = lower asymptote; c = inflection point; d = slope). For each participant, c was taken as the TBW, i.e. the point of decay of the illusion (Cecere et al., 2015).

To examine the SoA window, the number of times the individual reported that they caused the circle to appear on the screen was recorded. Thereafter, a sigmoid function was fitted to the data, determining each participant`s inflection point (corresponding to the width of the SoA window), in ms. A decreasing sigmoid function was used to fit the distribution of responses and was defined by the equation: $y = a+b/(1+exp(-(x-c)/d))$ (a = upper asymptote; b = lower asymptote; c = inflection point; d = slope). For each participant, c was taken as the SoA window, i.e. the point of decay of the self-attribution (Sato, 2009; Shimada et al., 2010).

Results

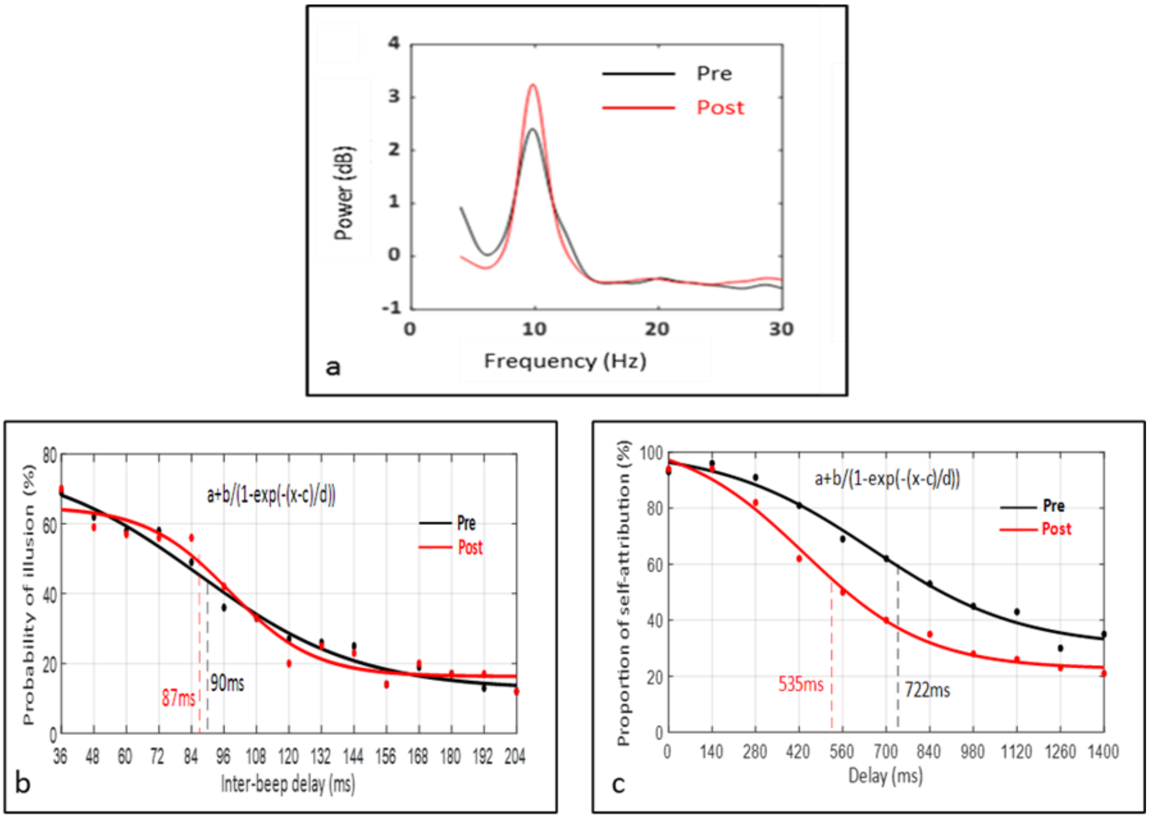

Figure 5.4: (a) Normalised average power spectrum over posterior area at rest with eyes closed across all participants at pre perceptual training. (b) Average percentage of probability of illusion plotted as a function of inter-beep delay. Data of each participant was first averaged for each inter-beep delay and hereafter across all participants according to the inter-beep delays. Data points represent the group average raw data. Curves represent the sigmoid fit determining the point of decay of the illusion, corresponding to the width of the TBW. (c) Average percentage of probability of self-attribution plotted as a function of delay. Data of each participant was averaged for each delay and hereafter across all participants according to the delays. Data points represent the group average raw data. Curves represent the sigmoid fit determining the point when the SoA judgement changes, corresponding to the width of the SoA window.

When considering the frequency of the occipital alpha peak, paired-samples t-test showed no significant difference between the frequency of the occipital alpha peak at post-perceptual training (M=10, SD=0.50) and at pre-perceptual training, (M=10.2, SD=1.02), *t(13)=0.56,* *p=.587*, d=0.15, Bayes Factor=4.31 (null versus alternative) (see Figure 5.4 a). A sensitivity power analysis showed that our sample size had 80% power to detect large effect sizes for t tests (dz=0. 81, α=.05, two-tailed). Similarly, there was no significant difference between the width of the TBW, at post-perceptual training (M=86, SD=27) and at pre-perceptual training, (M=90, SD=27), *t(8)=0.48,p=.646*, d=0.15, Bayes Factor=3.70 (null versus alternative) (see Figure 5.4 b). A sensitivity power analysis showed that our sample size had 80% power to detect very large effect sizes for t tests (dz=1.07, α=.05, two-tailed). However, when considering SoA window, paired-samples t-test showed a decreased width of the SoA window at post-perceptual training (M=535, SD=223) compared to pre-perceptual training, (M=722, SD=225), *t(10)=3.51,p =.006*, d=0.83, Bayes Factor=0.10 (null versus alternative) (see Figure 5.4 c). A sensitivity power analysis showed that our sample size had 80% power to detect large effect sizes for t tests (dz=0.94, α=.05, two-tailed).

Interim Discussion

Findings indicate a reduction of the SoA window following perceptual training, however, such a reduction was not observed in the case of TBW. In terms of alpha peak frequency, alpha oscillations remained unchanged following perceptual training. Before interpreting the above findings it should be considered that due to Covid-19 circumstances the laboratory-based testing had to cease. This resulted in sample of 14 out of pre-registered sample of 65. Moreover, due to exclusion of data sets judgement of agency task had final sample of 9 and double-flash illusion task had final sample of 10. Given the small sample size obtained confidence in the results is questionable. That is, the findings are susceptible of Type II error given the small sample size. Moreover, a sensitivity power analysis showed that our sample size had 80% power to detect large effect sizes for t tests. This coupled with the small effect sizes we obtained (alpha peak frequency: d=0.15, TBW: d=0.15) indicates that our study was considerably underpowered. Hence, it was decided to develop and conduct behavioural tasks of the current study online (EEG recording were not suitable for online base study).

Experiment 2 (Online Setting)

Method

Participants

The online sample consisted of 75 student volunteers from the University of Essex, recruited via the University research advertisement websites (i.e. SONA) with course credits as reimbursement. All participants had normal or corrected to normal vision and hearing to avoid these variables influencing the tasks. Participants gave their informed consent before taking part in the study. The study was approved by the local ethics committee and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki and approved by the University of Essex`s Faculty Ethics Subcommittee (departmental reference no: ETH2021-0206). Data is made accessible on a public repository - OSF via the following link: https://osf.io/u4x8v/?view_only=7802a3d16c8d4ad19044996769b704fa.

Data Exclusion

Fifty-five data sets were removed from double-flash illusion, 26 data sets were removed from the judgement of agency task and no data sets were removed from the EEG analysis. In double-flash illusion 35 data sets were excluded due to being completed online using Mac devises which distorted the task, such that only one tone was presented. This meant that participants could not experience the illusion. A further 20 data sets were excluded due to poor fit of the psychometric sigmoid function (R^2 less than .6) or/and incomplete data. In judgement of agency task all 26 excluded data sets were removed from further analysis due to poor fit of the psychometric sigmoid function (R^2 less than .6) or/and incomplete data.

Design

The current study used within-subjects design. The independent variable in the study was perceptual training with 2 conditions (pre-perceptual training and post-perceptual training). Dependent variables were the width of the TBW and the width of the SoA window measured at both conditions.

Apparatus/Materials

Perceptual training

The basic premise of the task was the same as that used in Experiment 1, with some small differences. Notably, the task was programmed and controlled by the INQUISIT Millisecond software package 5.0 (Millisecond Software, 2016) on an LCD monitor with a refresh rate of no less than 60Hz. Visual and auditory stimuli were 33.3ms in duration to ensure compatibility with majority of monitors (60Hz refresh rate, 16.6ms). Participants performed 3 equal sized blocks with 1-minute rest break in-between.

Double-flash illusion (measure of TBW)

The basic premise of the task was the same as that used in Experiment 1, with some minor differences. As with perceptual training, the task was programmed and controlled by the INQUISIT Millisecond software package 5.0 (Millisecond Software, 2016) on an LCD monitor with a refresh rate of no less than 60Hz. Visual and auditory stimuli were 33.3ms in duration to ensure compatibility with majority of monitors (60Hz refresh rate, 16.6ms). Stimulus Onset Asynchrony were between 32ms and 208ms, in steps of 16ms. These particular Stimulus Onset Asynchronies were also chosen to synchronize the stimulus timing with the refresh rate of the screen (60Hz, 16.6ms). Participants performed one block. Each Stimulus Onset Asynchrony was presented 28 times, for a total 308 trials.

Judgement of agency (measure of SoA)

The premise of the task was the same as that used in laboratory setting, with only difference being that the task was programmed and controlled by the INQUISIT Millisecond software package 5.0 (Millisecond Software, 2016).

Procedure

The study took place over 4 consecutive days. Participants were instructed to ensure that they were in a dimly lit room, were reminded to adjust the volume on their devices to a comfortable hearing level and were asked to sit approximately 60cm away from the computer screen with the plane of their eyes aligned to the centre of the monitor. Participants completed double-flash illusion task and judgement of agency task on Day 1 and Day 2. Perceptual training was completed on Day 2 and Day 3.

Data Analysis

Width of the TBW and width of the SoA window was assessed as in Experiment 1.

Results

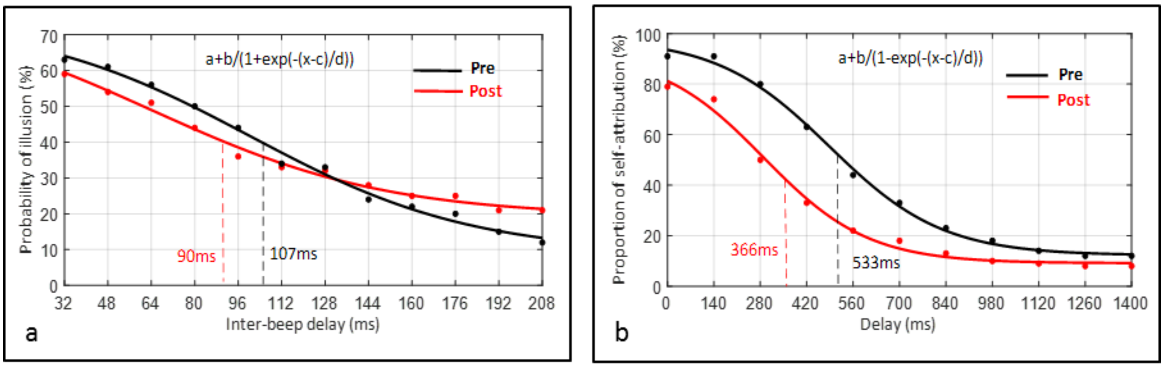

Figure 5.5: (a) Average percentage of probability of illusion plotted as a function of inter-beep delay. Data of each participant was first averaged for each inter-beep delay and hereafter across all participants according to the inter-beep delays. Data points represent the group average raw data. Curves represent the sigmoid fit determining the point of decay of the illusion, corresponding to the width of the TBW. (b) Average percentage of probability of self-attribution plotted as a function of delay. Data of each participant was averaged for each

delay and hereafter across all participants according to the delays. Data points represent the group average raw data. Curves represent the sigmoid fit determining the point when the SoA judgement changes, corresponding to the width of the SoA window.

In terms of the TBW, paired-samples t-test indicated that the width of the TBW is reduced at post-perceptual training (M=90, SD=36) compared to at pre perceptual training, (M=107, SD=26), *t(19)=2.23,p=.038*, d=0.55, Bayes Factor=0.694 (null versus alternative) (see Figure 5.5 a). A sensitivity power analysis showed that our sample size had 80% power to detect large effect sizes for t tests (dz=0.66, α=.05, two-tailed). Similarly, a paired-samples t-test showed decreased width of the SoA window at post-perceptual training (M=366, SD=181) compared to at pre perceptual training, (M=533, SD=186), *t(48)=7.70,p < .001*, d=0.91, Bayes Factor< .001 (null versus alternative) (see Figure 5.5 b). A sensitivity power analysis showed that our sample size had 80% power to detect medium effect sizes for t tests (dz=0.41, α=.05, two-tailed).

Interim Discussion

Despite the results indicating a reduction in the width of the TBW and SoA window following the perceptual training, the results cannot be accepted with certainty. It is possible that the observed reduction following perceptual training is due to the completion of the double-flash illusion task and judgement of agency task twice. In order to rule this out, a control condition should be introduced. Namely, novel sample of participants should perform the study without the aspect of perceptual training.

Experiment 3 (Control Condition)

Method

Participants

The control sample consisted of 20 volunteers recruited via social media platforms with £20 as reimbursement. All participants had normal or corrected to normal vision and hearing to avoid these variables influencing the tasks. Participants gave their informed consent before taking part in the study. The study was approved by the local ethics committee and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki and approved by the University of Essex`s Faculty Ethics Subcommittee (departmental reference no: ETH2021-0206). Data is made accessible on a public repository - OSF via the following link: https://osf.io/u4x8v/?view_only=7802a3d16c8d4ad19044996769b704fa.

Data Exclusion

From the control sample, ten data sets were removed from the double-flash illusion and five data sets were removed from the judgement of agency task. In double-flash illusion six data sets were excluded due to being completed online using Mac devises which distorted the task and 4 data sets were excluded due to poor fit of the psychometric sigmoid function (R^2 less than .6) or/and incomplete data. In the judgement of agency task, all five excluded data sets were removed from further analysis due to poor fit of the psychometric sigmoid function (R^2 less than .6) or/and incomplete data.

Design

The current study used within-subjects design. The independent variable in the study was the task itself (i.e. double-flash illusion task or judgement of agency task) with 2 conditions (day 1 and day 4). Dependent variables were the width of the TBW in case of double-flash illusion task and the width of the SoA window in case of judgement of agency task.

Apparatus/Materials

All materials and apparatus of both the double-flash illusion task and judgement of agency task were the same as in the Experiment 2.

<u>Procedure</u>

The protocol was the same as in Experiment 2 with only one difference. That is participants did not complete perceptual training and instead had rest days on Day 2 and Day 3.

<u>Data Analysis</u>

Width of the TBW and width of the SoA window was assessed as in Experiment 1 and 2.

Results

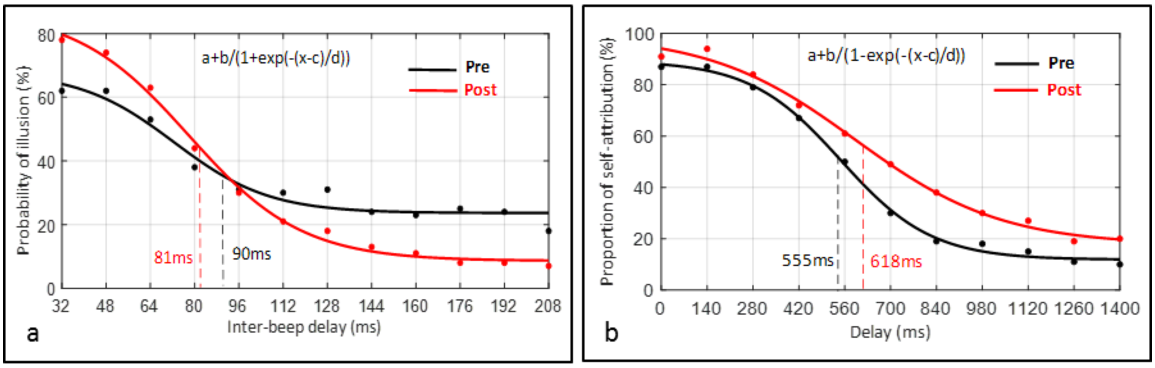

Figure 5.6: (a) Average percentage of probability of illusion plotted as a function of inter-beep delay. Data of each participant was first averaged for each inter-beep delay and hereafter across all participants according to the inter-beep delays. Data points represent the group average raw data. Curves represent the sigmoid fit determining the point of decay of the illusion, corresponding to the width of the TBW. (b) Average percentage of probability of self-attribution plotted as a function of delay. Data of each participant was averaged for each delay and hereafter across all participants according to the delays. Data points represent the group average raw data. Curves represent the sigmoid fit determining the point when the SoA judgement changes, corresponding to the width of the SoA window.

Paired-samples t-tests showed that without perceptual training the width of the TBW did not differ significantly between the first (M=90, SD=41) and the second measure (M=81, SD=23) of the double-flash illusion task, $t(9)=0.91, p=.385$, d=0.29, Bayes Factor=2.94 (null versus alternative) (see Figure 5.6 a). A sensitivity power analysis showed that our sample size had

80% power to detect very large effect sizes for t tests (dz=1.00, α=.05, two-tailed). Likewise, paired-samples t-test showed that without perceptual training the width of the SoA window did not differ significantly between the first (M=555, SD=143) and the second measure (M=618, SD=212) of the judgement of agency task, *t(14)=-1.56,p=.141*, d=0.40, Bayes Factor=1.76 (null versus alternative) (see Figure 5.6 b). A sensitivity power analysis showed that our sample size had 80% power to detect large effect sizes for t tests (dz=0.81, α=.05, two-tailed).

Next, to assess the effect of perceptual training on TBW and SoA window, we combined the data from experiment 2 and 3 to conduct a two-way mixed ANOVA with time (day 1 versus day 4), and group type (perceptual training versus control) as the two factors. The results showed that there was significant main effect of time on the width of the SoA window, *F(1, 62)=5.26,p =.025*, η_p^2=.078, with the width of the SoA window at day 4 being narrower that the width of the SoA window at day 1. Similarly, there was significant main effect of group type on the width of the SoA window, *F(1, 62)=7.80,p=.007*, η_p^2=.112, with participants showing narrower SoA window for control group than perceptual training group. There also was a significant interaction between time and group type, *F(1, 62)=26,p<.001*, η_p^2=.295, indicating that the change in SoA window was significantly different between the perceptual training group and the control group. In terms of TBW, the results of the two-way mixed ANOVA showed that there was significant main effect of time on the width of the TBW, *F(1, 28)=4.25,p=.049*, η_p^2=.132, with the width of the TBW at day 4 being narrower that the width of the TBW at day 1. There was non-significant main effect of group type on the width of the TBW, *F(1, 28)=1.60,p=.217*, η_p^2=.054, with participants showing similar average TBW for perceptual training group and control group. There was also a non-significant interaction between time and group type, *F(1, 28)=0.43,p=.519*, η_p^2=.015, indicating that TBW of both groups was similar at day 1 and day 4. A sensitivity power analysis showed that our sample size had 80% power to detect small effect sizes for two-way ANOVA ($f = 0.15$; $\alpha = 0.05$, two-tailed).

Interim Discussion

As can be seen from the results, the SoA window is reduced following perceptual training. Whereas, in contrast such a reduction effect is not observed without perceptual training. Moreover, it was shown that SoA window differed between the perceptual training group and control groups at day 1 and day 4, providing higher confidence in the conclusion that SoA window is reduced following perceptual training. Similarly, TBW is reduced following perceptual training with such reduction not being observed without perceptual training. However, TBW of the perceptual training group and control group was shown to be similar at day 1 and day 4. Hence, making it difficult to state with confidence that perceptual training rather than completing double-flash illusion twice caused the reduction in the TBW. Nevertheless, it seems that TBW of the groups was shown to be similar at day 1 and day 4, possibly due to the small sample size (A sensitivity power analysis showed that our sample size had 80% power to detect small effect sizes for two-way ANOVA ($f = 0.15$; $\alpha = 0.05$, two-tailed. Thus, indicating underpowered study.) and large variability between participants. It appears that reduction of the TBW in the perceptual training group was not strong enough to lead to a significant difference between the perceptual training group and control group. However, to rule out that completing the double-flash illusion twice caused the reduction of the TBW rather than perceptual training, the current study should be completed with larger sample.

Discussion

The aim of the current study was to examine whether perceptual training affects TBW, SoA and the frequency of the occipital alpha peak similarly. That is, whether the width of the

TBW and the width of the SoA window reduces and frequency of the occipital alpha peak increases following perceptual training. Findings indicated that both the SoA window and the TBW were reduced after perceptual training. However, the frequency of the occipital alpha peak did not change after perceptual training.

Current findings regarding TBW are in line with predominant stance of the existing literature (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019) showing a reduction of the width of the TBW following the perceptual training. More precisely, De Niear et al. (2018) and Stevenson et al. (2013) showed a reduction in TBW immediately after perceptual training. Whereas, Powers et al. (2009) and Zerr et al. (2019) extended these findings to stable reduction of the TBW at least a week after the perceptual training. Similarly, findings regarding the SoA window are in line with existing literature. Namely, the notion that SoA and temporal sensitivity are linked (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989) and also the view that SoA window, like the TBW (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019), is reduced after perceptual training. However, it must be noted that a later study by Powers et al., (2016) did not find cognitive processes to be altered by perceptual training a week after perceptual training. The above leads one to conclude that perhaps changes in cognitive processes diminish after approximately a week. The reasoning behind such a conclusion is that for learning to become permanent it should be established within a neural system (Swart et al., 2015). That is, if one considers that the neural system drives cognitive processes, any changes in cognitive processes in response to learning and development can only be sustained permanently if corresponding neural mechanisms have also been changed permanently. It has been indicated that considerable amount of learning and development (three or more months) is required to achieve permanent neural changes (Swart et al., 2015). Given that our study employed only brief perceptual training we would not expect permanent neural changes. Instead, we would expect neural changes to be temporary and fading as time progresses. Given Powers et al. (2016) findings and existing literature in neuroplasticity (Swart et al., 2015) it can be argued that neural changes fade within approximately a week and consequently so does the changes in corresponding cognitive processes. Our findings in relation to the SoA window is a novel discovery, indicating that perceptual training can alter not only lower cognitive processes (i.e. TBW) but can also affect higher cognitive processes (i.e. SoA). Moreover, our findings propose explanation for fading effects of perceptual training observed in previous literature.

Given the above, findings showing that the alpha peak frequency was unchanged immediately after perceptual training are at first unexpected and surprising. As previously discussed, the previous evidence leans suggests that the speed of occipital alpha oscillations is the neural mechanism underlying temporal sensitivity (Gibbon et al., 1984; Glicksohn et al., 2009; Horr et al., 2016; Luft & Bhattacharya, 2015; Mioni et al., 2020; Treisman, 1963; Treisman, 2013; Wittmann & Van Wassenhove, 2009; Wittmann et al., 2010). More specifically, higher temporal sensitivity has been associated with a higher frequency of the occipital alpha peak (Kononowicz & Van Wassenhove, 2016; Samaha & Postle, 2015). Additional evidence comes from studies investigating this relationship via assessment of TBW (Cecere et al., 2015; Migliorati et al., 2020, Venskus & Hughes, 2021, chapter two in this thesis) and SoA window (Venskus et al., 2021, chapter three in this thesis). Hence, it was expected that by modification of temporal sensitivity its neural mechanism would be similarly modified.

When considering the study of Migliorati et al. (2020), they measured the width of the TBW via a visuotactile simultaneity judgment task while recording electrophysiological activity of the occipital alpha peak. It was found that a faster frequency of the occipital alpha peak accounted for narrower width of the TBW. Here the alpha peak frequency and the width of the TBW seem to be related. This leads to the possible conclusion that the alpha peak frequency is driving the width of the TBW. Namely, increased alpha peak frequency results in narrower excitatory phase in turn leading to higher temporal sensitivity (Kononowicz & Van Wassenhove, 2016; Samaha & Postle, 2015). Whereas, higher temporal sensitivity results in shorter width of the TBW (see Hirst et al., 2020; Keil, 2020 for recent reviews). In the study conducted by Cecere et al. (2015) and Venskus et al. (2021, chapter three in this thesis), the alpha peak frequency was modified by tACS while the width of the TBW (Cecere et al., 2015, Venskus et al., 2021, chapter three in this thesis) and SoA window (Venskus et al., chapter three in this thesis) was measured. More specifically, individual`s alpha peak frequency was either increased (+2Hz) or decreased (-2Hz) while tasks measuring temporal windows were undertaken. Results indicated that increased alpha peak frequency led to decreased with of the TBW as well as SoA window and vice versa. This provides initial causal evidence for the idea that TBW and, to a lesser degree, the SoA window, are being driven by the alpha peak frequency. In other words, tACS alters the alpha peak frequency which in turn determines temporal sensitivity and consequently to a degree width of the TBW and SoA.

The current study did not measure the individual’s natural alpha peak frequency nor did it modify the frequency by direct stimulation. Instead, it measured the alpha peak frequency before and after brief (1 hour per day on 2 consecutive days) perceptual training. Perceptual training can be argued to alter the alpha peak frequency due to being the proposed neural mechanism of temporal sensitivity. That is, as temporal sensitivity has been shown to be modifiable via perceptual training, by shifting PSS towards the optimum (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019), its neural mechanism (alpha peak frequency) should similarly be affected.

Given the current study found changes in cognitive processes immediately following perceptual training and notion that alpha peak frequency is driving these cognitive changes (Cecere et al., 2015; Migliorati et al., 2020, Venskus & Hughes, 2021, chapter two in this thesis; Venskus et al., 2021, chapter two in this thesis), we would expect to find alpha peak frequency to have changed immediately following perceptual training. However, the current study did not find a significant change in alpha peak frequency following perceptual training. One explanation could be that other neural substrates than alpha peak frequency are driving the cognitive changes observed as there clearly should be changes that are occurring within neural networks that are driving the corresponding cognitive changes. Nevertheless, such explanation is somewhat unlikely given the vast evidence supporting the notion that alpha peak frequency is the neural substrate for temporal sensitivity (Cecere et al., 2015; Migliorati et al., 2020, Venskus & Hughes, 2021, chapter two in this thesis) and SoA (Venskus et al., 2021, chapter three in this thesis). More convincing explanation for the lack of change in alpha peak frequency following perceptual training could be found by considering the small sample size obtained (N=14) in Experiment 1 where alpha frequency was measured. That is, the findings are susceptible of Type II error given the small sample size. Moreover, a sensitivity power analysis showed that our sample size had 80% power to detect large effect sizes for t tests. This coupled with the small effect sizes we obtained (d=0.15) indicates that our study was considerably underpowered. Given the above it is not surprising that we did not find significant change in alpha peak frequency following perceptual training. The above also leads to suggestion that perhaps we would have observed significant change in alpha peak frequency if the study was not underpowered. However, to be sure of such conclusions, longitudinal studies with appropriate power should explore the effects of perceptual training on the alpha peak frequency, TBW and SoA window.

Conclusions

The current study aimed to examine whether perceptual training affects TBW, SoA and the alpha peak frequency similarly. That is, whether the width of the TBW and the width of the SoA window reduces and alpha peak frequency increases following perceptual training. We found that TBW and SoA window was reduced immediately after a brief perceptual training. But alpha oscillations stayed unchanged. We explain findings in terms of neuroplasticity (Buonomano & Merzenich, 1998; Demarin & Morovic, 2014; Shaw, 2001) and characteristics of our study.

Chapter Six: General Discussion

Study summaries

Individual differences in alpha frequency are associated with the time window of multisensory integration, but not time perception.

We built this study on the previously shown relationship between TBW and time perception (Droit-Volet, 2008; Fenner et al., 2020; Hillock-Dunn & Wallace, 2012; Wang et al., 2005). Namely, it has been shown that children have a larger filled-empty difference (Droit-Volet, 2008) and a wider TBW than adults (Hillock-Dunn & Wallace, 2012; Wang et al., 2005), indicating an association between these processes. More importantly, Fenner et al. (2020) measured both TBW and time perception and found a positive correlation between the width of the TBW and the magnitude of the filled duration illusion. In addition, alpha peak frequency has been proposed to be the neural mechanism for both processes. Alpha oscillations have previously been linked to both the TBW (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020; Samaha & Postle, 2015) and time perception (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020). In turn, the conceptualization behind the link of alpha oscillations with time perception (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020) and TBW (Cecere et al., 2015; Hirst et al., 2020; Keil, 2020; Keil & Senkowski, 2017; Migliorati et al., 2020) is argued to be the internal clock model (a hypothetical mechanism that is driven by a neural pacemaker producing rhythm; Kononowicz & Van Wassenhove, 2016). However, the association between TBW, time perception and alpha oscillations is not well established. Hence, we focused on exploring to what degree, if any, time perception, the TBW and the alpha peak frequency are related. We observed a significant relationship between the TBW and peak alpha frequency but not alpha power. However, time perception was not linked with either of these. These findings were discussed with respect to the possible underlying mechanisms of multisensory integration and time perception.

Temporal binding window and sense of agency are related processes modifiable via occipital tACS.

The construct for this study was derived from research indicating that temporal cues and multisensory integration play a role in SoA (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989). The TBW refers to the time frame within which temporal grouping of sensory information takes place (Colonius & Diederich, 2004) and is highly variable between individuals (Cecere et al., 2015; Ferri et al., 2018; Haß et al., 2017). Given the above it is plausible that individual differences in the TBW and SoA are associated. However, only one previous study had directly assessed whether individual differences in the TBW and SoA are associated. Venskus et al. (2021; experiments 1 and 2) found that TBW positively correlated with SoA. Moreover, if temporal grouping of sensory information links TBW and SoA, it is plausible that these two processes also have a common underlying neural mechanism with one strong candidate being alpha peak frequency. Indeed, the previous literature contains studies linking alpha peak frequency with TBW (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020) and indirectly indicate that alpha peak frequency may also be linked with SoA (Farrer et al., 2008; Farrer et al., 2013; Fenner et al., 2020; Glicksohn et al., 2009; Horr et al., 2016; Kawabe et al., 2013; Knoblich & Kircher, 2004; Mioni et al., 2020; Shanks et al., 1989). Given that existing literature lacks studies directly exploring the link between SoA and frequency of the alpha peak, the main focus of our study was to explore such a relationship by examining whether occipital tACS stimulation alters the width of the SoA window as well as the TBW. Additionally, we also aimed to accumulate evidence in relation to the degree to which individual differences in the TBW correlate with individual differences in the SoA window. Unexpectedly, the TBW and the SoA window were shown not to be associated. However, these processes were both modulated by applying occipital tACS at either 14Hz or 8Hz. We found 14Hz tACS stimulation was associated with narrower TBW and SoA window. Overall, our results suggest the TBW and the time window of SoA are partially related. They also point towards a possible underlying neural mechanism (alpha peak frequency) for this association.

The relationship between temporal sensitivity and sense of agency.

This study builds directly on the findings of Venskus et al. (2021, chapter three of this thesis) showing that SoA and TBW are linked in a simple action-outcome task. More specifically, that a wider SoA window is associated with a wider TBW. Our study aimed to explore how complex action-outcome relationships in metacognition of agency link to TBW. We used the metacognition of agency task (Metcalfe & Greene, 2007), where participants played a space invaders-type game requiring them to catch Xs and avoid Os as they descend down the screen. On each trial, we manipulated either the lag between the participants action and the movement of the on-screen cursor, or we introduced noise (turbulence) to the movement. The degree to which these manipulations influence participants self-reported control, acts as the measure of metacognition of agency. We evaluated whether the metacognition of agency correlated with individual differences in TBW. We found an association only during long lag manipulations. Here, in contrast to our predictions, we observed that increased sensitivity of metacognition of agency was associated with wider TBW. We concluded that the relationship between TBW and SoA observed in previous studies is less prevalent in complex action-outcome relationships where metacognition of agency is involved as they present wider range of possible agency cues. That is, in presence of other agency cues and wider TBW, metacognition of agency may depend more on these other cues than temporal cues.

Perceptual training modifies temporal binding window and sense of agency but not alpha oscillations.

This study was derived from previous studies in this thesis as well as previous literature on the topic as discussed in the general introduction. Existing literature suggests that perceptual training can modify temporal sensitivity (the ability to detect time-based discrepancy between two stimuli) (De Niear et al., 2018; Powers et al., 2009; Stevenson et al., 2013; Zerr et al., 2019). More precisely, a reduction in the width of the TBW is observed following perceptual training. Given this, it is also reasonable to speculate that as perceptual training affects temporal sensitivity, its proposed neural mechanism - frequency of alpha peak (Cecere et al., 2015; Hirst et al., 2020; Keil, 2020; Keil & Senkowski, 2017; Migliorati et al., 2020) should similarly be affected. Moreover, if to assume that temporal sensitivity is affecting SoA (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989) in simple action-outcome relationship (Venskus et al., 2021, chapter three of this thesis) and appears to be linked to the frequency of the alpha peak (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020; Venskus et al., 2021, chapter three of this thesis) one can conclude that enhancing temporal sensitivity via perceptual training would respectively modify SoA. Similarly, as previous literature has linked time perception to temporal sensitivity (Droit-Volet, 2008; Fenner et al., 2020; Wang et al., 2005) and frequency of alpha peak (Glicksohn et al., 2009; Horr et al., 2016; Mioni et al., 2020) it seems that perceptual training is likely to also modify time perception. However, time perception was not included in this study. The reasoning behind such decision stems from the fact that this thesis did not find time perception being associated with either TBW or alpha frequency (see chapter two). More specifically, we argued that the relationship between time perception and TBW is mediated by explicit thinking about time. Similarly, we argued that the specifics of the tasks mediate the association between time perception and alpha oscillations. Despite the likelihood of perceptual training modifying the frequency of alpha peak and SoA existing literature lacks such studies. Therefore, this study explored the effects of perceptual training on SoA and frequency of the alpha peak as well as aimed to replicate the previously reported effects of perceptual training on TBW. Findings indicated that the SoA window, like the TBW, was reduced after perceptual training. However, the frequency of the occipital alpha peak did not change after perceptual training. We explain findings in terms of structural neuroplasticity (Buonomano & Merzenich, 1998; Demarin & Morovic, 2014; Shaw, 2001) and characteristics of the study.

Implications

Firstly, the research presented in this thesis provides the opportunity to reaffirm evidence presented in the few existing studies to date indicating that the TBW and the alpha peak frequency are related (Cecere et al., 2015; Keil & Senkowski, 2017; Migliorati et al., 2020; Samaha & Postle, 2015). Furthermore, this thesis in combination with the notion that alpha power and alpha frequency are distinctive (Benwell et al., 2019) extends current knowledge by allowing to conclude that TBW is linked to alpha peak frequency but not alpha power.

In terms of time perception, this thesis is the first to propose that the relationship between time perception and the TBW depends on whether the measures are obtained implicitly or explicitly. More specifically, the relationship between time perception and the TBW is mediated by the explicit nature of the tasks. In addition, this thesis allows us to propose that crucial to the correlation between time perception and alpha oscillations is the specifics of the tasks used.

When considering our findings in relation to SoA, one key implication is that they point towards the importance of incorporating in the conclusions the notion that although a significant aspect of both the TBW (Colonius & Diederich, 2012; Dixon & Spitz, 1980; King, 2005; Lewkowicz & Ghazanfar, 2009; Spence & Squire, 2003; Van Wassenhove et al., 2007; Vatakis, 2013; Vroomen & Keetels, 2010) and the SoA window (Farrer et al., 2008; Farrer et al., 2013; Kawabe et al., 2013; Knoblich & Kircher, 2004; Shanks et al., 1989) is the temporal grouping of sensory information, this connection is stronger for the TBW compared to SoA window. More specifically, it is argued that despite SoA likely being informed by cues related to temporal integration (Chambon et al., 2014; Chambon & Haggard, 2012; Frith et al., 2000; Moore & Fletcher, 2012; Wegner, 2002; Wenke et al., 2010), and therefore will relate to the TBW, this relationship is inevitably incomplete. Moreover, in the presence of other agency cues and a wider TBW, SoA may depend more on these other cues than temporal cues. Another significant implication in relation to SoA, stems from findings indicating that the occipital tACS stimulation at the upper bound of the alpha frequency range (14Hz), reduced the width of both the TBW and the SoA window, compared to stimulation at the lower bound of the alpha range (8Hz). That is, the research in this thesis is the first to provide evidence that alpha peak frequency is related to the SoA window when simple action-outcome relationships are considered. Moreover, evidence is obtained showing that the association between alpha peak frequency and SoA is weaker than that with TBW. This is explained to be due to the SoA relaying on numerous other cues in addition to temporal ones.

Finally, an investigation of the effects of perceptual training presents novel findings indicating that perceptual training alters SoA but alpha frequency remains unchanged. We explain these findings in terms of structural neuroplasticity (Buonomano & Merzenich, 1998; Demarin & Morovic, 2014; Shaw, 2001) and characteristics of the study.

Limitations and further directions

In regard to time perception and TBW, as previously discussed, this thesis argues in favor of the notion that the relationship between time perception and the TBW is mediated by the explicit nature of the tasks. That is, shared common underlying process (i.e. explicitly thinking about time) in filled duration illusion and simultaneity judgment task mediated the relationship between time perception and TBW. Future research should explore this possibility in more detail. For instance, a range of explicit and implicit tasks could be utilized in order to gain more clarity in terms of the specific task characteristics that mediate the relationship between time perception and TBW.

Despite proposing that crucial to the correlation between time perception and alpha oscillations is the specifics of the tasks used, this thesis does not incorporate a range of different tasks. More specifically, it is argued that contradictory findings of this thesis and of Horr et al. (2016) could be due to discrepancy of characteristics of the intervals in the filled duration illusion: This thesis used either entirely filled or empty durations, whereas Horr et al. (2016) used regularly or irregularly spaced tones. It was then taken further and suggested that it is possible that the spaced tones in Horr et al. (2016) triggered neural entrainment that can drive distortions in time perception, and that these in turn might be mediated by alpha oscillations (Matthews et al., 2014). Further research is required to fully understand why this difference might be crucial to the correlation with alpha oscillations. One way to shed some light on the topic would be to develop a task that utilizes intervals with regularly or irregularly spaced tones and explore their association with alpha oscillations.

When considering SoA, this thesis argues that as SoA depends on many different cues in addition to temporal cues (Chambon et al., 2014; Chambon & Haggard, 2012; Frith et al., 2000; Moore & Fletcher, 2012; Wegner, 2002; Wenke et al., 2010); one might also expect this to vary in different contexts (Sidarus et al., 2017). In this thesis compared to Venskus et al. (2021; experiment 1 and 2), study participants were receiving continuous tACS stimulation while completing the judgment of agency task. As such, it is possible that the presence of tACS stimulation may have been responsible for removing the association between the TBW and the SoA window in our study either directly, as a result of stimulating the brain (Hughes, 2018), or indirectly, as a result of the change in context (Sidarus et al., 2017). Further research should investigate this possible explanation in more detail, for instance by including additional baseline conditions and/or sham stimulation conditions. Moreover, it is proposed that the relationship between TBW and SoA is less prevalent in complex action-outcome relationships where metacognition of agency is involved, as they present wider range of possible agency cues. That is, in the presence of other agency cues and a wider TBW, metacognition of agency may depend more on these other cues than temporal cues (see chapter four for more detailed discussion). Further research should undertake more detailed investigation of this explanation. For instance, the performance of individuals with wide and narrow TBWs could be compared over different lag and turbulence conditions. This would show whether those with wider TBW are more influenced by the manipulations and whether this influence is stronger as the strength of the manipulations increases.

It is also important to note that this thesis makes claims based on assumption that tACS has directly influenced alpha frequency. That is, the occipital tACS stimulation at the upper bound of the alpha frequency range (14Hz), reduced the width of both the TBW and the SoA window, compared to stimulation at the lower bound of the alpha range (8Hz). However, as this thesis did not employ a tACS condition at any other electrode locations (a control condition), it is not possible to rule out the possibility that the tACS modulation was not directly related to the alpha frequency. tACS stimulation of the peripheral nerves could cause tactile sensation, which in turn could then drive the effect of the stimulation as opposed to the alpha frequency. To ensure that sub-threshold tactile sensation is not interfering with the findings (in this and other studies), further research should add a control condition (using different montage, i.e. stimulation excluding modulation of the frequency of the occipital alpha peak) to rule out more generalized effects of tACS simulation.

In terms of effects of perceptual training on TBW, this thesis showed that the width of the TBW is reduced following perceptual training. This reduction was not observed in the absence of perceptual training. However, the width of the TBW of the experimental and control groups was shown to be similar at first and second measure. Therefore, confidence in the results stating that perceptual training rather than completing double-flash illusion twice caused the reduction of the TBW is decreased. Here it was argued that the TBW of the experimental and control group was similar due to the small sample size and large variability between participant's TBWs (due to COVID-19 preventing laboratory-based studies). Thus, the reduction of the TBW in the experimental group was not strong enough to lead to significant difference between the experimental and control group. However, to rule out that completing double-flash illusion twice caused the reduction of the TBW rather than perceptual training further studies should explore effects of perceptual training on TBW with a larger sample size.

Finally, this thesis argued that for cognitive changes to become permanent they should be established within a neural system (Swart et al., 2015). That is, if to consider that neural system drives cognitive processes any changes in cognitive processes in response to learning and development can only be sustained permanently if corresponding neural mechanisms have also been changed. It has been indicated that considerable amount of learning and development (three or more months) is required to achieve neural changes (Swart et al., 2015). Given the above, it seems one should expect to observe changes in cognitive processes (TBW and SoA window) immediately following short perceptual training with such effect fading as time progresses. However, to be sure of such conclusions longitudinal studies should explore the effects of perceptual training on the alpha peak frequency, TBW and SoA window.

Conclusions

The first three studies in this thesis focused on exploring the relationship between TBW, time perception and SoA while also considering alpha oscillations as their potential neural mechanism. From the findings it was concluded that TBW and SoA in simple action-outcome relationships are related processes with alpha oscillations being potential shared neural mechanism. Yet, in complex action-outcome relationships where metacognition of agency is involved, this link is less prevalent, as they present a wider range of possible agency cues that are relied upon instead of temporal cues. However, time perception was concluded not to be associated with either. The observed relationships were then investigated further via perceptual training in the fourth study. Here we found that TBW and SoA window were modified by brief perceptual training but alpha oscillations stayed unchanged. We explain these findings in terms of structural neuroplasticity and characteristics of the study.

The grouping of temporal information is paramount in the accurate perception of the environment. Despite some limitations, this thesis provides significant novel contributions to understanding the relationship between temporal sensitivity and other cognitive processes, as well as their neural basis. It also provides a rich diversity of avenues for possible future research in this field.

References

Baijal, S., & Srinivasan, N. (2010). Theta activity and meditative states: spectral changes during concentrative meditation. *Cognitive Processing*, 11(1), 31-38. https://doi.org/10.1007/s10339-009-0272-0.

Basharat, A., Adams, M. S., Staines, W. R., & Barnett-Cowan, M. (2018). Simultaneity and temporal order judgments are coded differently and change with age: An event-related potential study. *Frontiers in Integrative Neuroscience, 12,* 15. https://doi.org/10.3389/fnint.2018.00015.

Benwell, C. S., London, R. E., Tagliabue, C. F., Veniero, D., Gross, J., Keitel, C., & Thut, G. (2019). Frequency and power of human alpha oscillations drift systematically with time-on-task. *NeuroImage, 192,* 101-114. https://doi.org/10.1016/j.neuroimage.2019.02.067.

Bizo, L. A., Chu, J. Y., Sanabria, F., & Killeen, P. R. (2006). The failure of Weber's law in time perception and production. *Behavioural Processes*, 71(2-3), 201-210. https://doi.org/10.1016/j.beproc.2005.11.006.

Boenke, L. T., Deliano, M., & Ohl, F. W. (2009). Stimulus duration influences perceived simultaneity in audiovisual temporal-order judgment. *Experimental Brain Research*, 198(2-3), 233-244. https://doi.org/10.1007/s00221-009-1917-z.

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, 25(1), 49-59. https://doi.org/10.1016/0005-7916(94)90063-9.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433-436. https://doi:10.1163/156856897x00357.

Buehner, M. J., & Humphreys, G. R. (2009). Causal binding of actions to their effects. *Psychological Science*, 20(10), 1221-1228. https://doi.org/10.1111/j.1467-9280.2009.02435.

Buffardi, L. (1971). Factors affecting the filled-duration illusion in the auditory, tactual, and visual modalities. *Perception & Psychophysics*, 10(4), 292-294. https://doi.org/10.3758/BF03212828.

Buonomano, D. V., & Merzenich, M. M. (1998). Cortical plasticity: from synapses to maps. *Annual Review of Neuroscience, 21*(1), 149-186. https://doi.org/10.1146/annurev.neuro.21.1.149.

Busch, N. A., Dubois, J., & Van Rullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *Journal of Neuroscience*, 29(24), 7869-7876. https://doi.org/10.1523/JNEUROSCI.0113-09.2009.

Calomeni, M. R., da Silva, V. F., Velasques, B. B., Feijó, O. G., & Bittencourt, J. M. (2017). Modulatory effect of association of brain stimulation by light and binaural beats in specific brain waves. *Clinical Practice and Epidemiology in Mental Health: CP & EMH*, 13, 134. https://doi: 10.2174/1745017901713010134.

Cecere, R., Rees, G., & Romei, V. (2015). Individual differences in alpha frequency drive crossmodal illusory perception. *Current Biology*, 25(2), 231-235. https://doi.org/10.1016/j.cub.2014.11.034.

Chambon, V., & Haggard, P. (2012). Sense of control depends on fluency of action selection, not motor performance. *Cognition*, 125(3), 441-451. https://doi.org/10.1016/j.cognition.2012.07.011.

Chambon, V., Sidarus, N., & Haggard, P. (2014). From action intentions to action effects: how does the sense of agency come about? *Frontiers in Human Neuroscience*, 8, 320. https://doi.org/10.3389/fnhum.2014.00320.

Church, R. M. (1984). Properties of the internal clock. *Annals of the New York Academy of Sciences*, 423(1), 566-582. https://doi.org/10.1111/j.1749-6632.1984.tb23459.x.

Cohen, M. X. (2011). It's about time. *Frontiers in Human Neuroscience*, 5, 1-15. https://doi.org/10.3389/fnhum.2011.00002.

Colonius, H., & Diederich, A. (2004). Multisensory interaction in saccadic reaction time: A time-window-of-integration model. *Journal of Cognitive Neuroscience*, 16(6), 1000-1009. https://doi.org/10.1162/0898929041502733.

Colonius, H., & Diederich, A. (2012). Focused attention vs. crossmodal signals paradigm: Deriving predictions from the time-window-of-integration model. *Frontiers in Integrative Neuroscience*, 6, 62. https://doi.org/10.3389/fnint.2012.00062.

Coren, S., Ward, L. M., & Enns, J. T. (1999). *Sensation and perception* (5^{th} ed.). Harcourt College Pub.

De Niear, M. A., Gupta, P. B., Baum, S. H., & Wallace, M. T. (2018). Perceptual training enhances temporal acuity for multisensory speech. *Neurobiology of Learning and Memory*, 147, 9-17. https://doi.org/10.1016/j.nlm.2017.10.016.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009.

Demarin, V., & Morovic, S. (2014). Neuroplasticity. *Periodicum Biologorum*, 116(2), 209-211.

Dixon, N. F., & Spitz, L. (1980). The detection of auditory visual desynchrony. *Perception*, 9(6), 719-721. https://doi.org/10.1068/p090719.

Doidge, N. (2007). *The brain that changes itself: Stories of personal triumph from the frontiers of brain science* (Reprint ed.). Penguin Books.

Donoghue, T., Haller, M., Peterson, E. J., Varma, P., Sebastian, P., Gao, R., et al. (2020). Parameterizing neural power spectra into periodic and aperiodic components. *Nature Neuroscience*, 1–24. https://doi.org/10.1038/s41593-020-00744-x.

Doty, R. L. (2015). *Handbook of olfaction and gustation.* John Wiley & Sons.

Droit-Volet, S. (2008). A further investigation of the filled-duration illusion with a comparison between children and adults. *Journal of Experimental Psychology: Animal Behavior Processes*, 34(3), 400. https://doi.org/10.1037/0097-7403.34.3.400.

Droit-Volet, S., & Meck, W. H. (2007). How emotions colour our perception of time. *Trends in Cognitive Sciences*, 11(12), 504-513. https://doi.org/10.1016/j.tics.2007.09.008.

Engbert, K., Wohlschlager, A., Thomas, R., & Haggard, P. (2007). Agency, subjective time, and other minds. *Journal of Experimental Psychology: Human Perception and Performance*, 33(6), 1261-1268. https://doi:10.1037/0096-1523.33.6.1261

Engel, G. R., & Dougherty, W. G. (1971). Visual-auditory distance constancy. *Nature*, 234(5327), 308-308. https://doi.org/10.1038/234308a0.

Farrer, C., Bouchereau, M., Jeannerod, M., & Franck, N. (2008). Effect of distorted visual feedback on the sense of agency. *Behavioural Neurology*, 19(1, 2), 53-57. doi: 10.1155/2008/425267.

Farrer, C., Valentin, G., & Hupe, J.M. (2013). The time windows of the sense of agency. *Consciousness and Cognition*, 22, 1431-1441. https://doi.org/10.1016/j.concog.2013.09.010.

Fenner, B., Cooper, N., Romei, V., & Hughes, G. (2020). Individual differences in sensory integration predict differences in time perception and individual levels of schizotypy. *Consciousness and Cognition*, 84, 102979. https://doi.org/10.1016/j.concog.2020.102979.

Ferri, F., Venskus, A., Fotia, F., Cooke, J., & Romei, V. (2018). Higher proneness to multisensory illusions is driven by reduced temporal sensitivity in people with high schizotypal traits. *Consciousness and Cognition*, 65, 263-270. https://doi.org/10.1016/j.concog.2018.09.006.

Foley, A. J., Michaluk, L. M., & Thomas, D. G. (2004). Pace alteration and estimation of time intervals. *Perceptual and Motor Skills*, 98(1), 291-298. https://doi.org/10.2466/pms.98.1.291-298.

Franck, N., Farrer, C., Georgieff, N., Marie-Cardine, M., Daléry, J., d'Amato, T., & Jeannerod, M. (2001). Defective recognition of one's own actions in patients with schizophrenia. *American Journal of Psychiatry*, 158(3), 454-459. https://doi.org/10.1176/appi.ajp.158.3.454.

Frith, C. D., Blakemore, S., & Wolpert, D. M. (2000). Explaining the symptoms of schizophrenia: Abnormalities in the awareness of action. *Brain Research Reviews*, 31(2-3), 357-363. https://doi.org/10.1016/S0165-0173(99)00052-1.

Frith, C., & Dolan, R. (1996). The role of the prefrontal cortex in higher cognitive functions. *Cognitive Brain Research*, 5(1-2), 175-181. https://doi.org/10.1016/S0926-6410(96)00054-7.

Fujisaki, W., & Nishida, S. Y. (2009). Audio–tactile superiority over visuo–tactile and audio–visual combinations in the temporal resolution of synchrony perception. *Experimental Brain Research*, 198(2-3), 245-259. https://doi.org/10.1007/s00221-009-1870-x.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of Sciences*, 423(1), 52-77. https://doi.org/10.1111/j.1749-6632.1984.tb23417.x.

Gil, S., & Droit-Volet, S. (2012). Emotional time distortions: The fundamental role of arousal. *Cognition and Emotion*, 26(5), 847-862. https://doi.org/10.1080/02699931.2011.625401.

Glicksohn, J., Ohana, A. B., Dotan, T. B., Goldstein, A., & Donchin, O. (2009). Time production and EEG alpha revisited. *NeuroQuantology*, 7(1). https://doi.org/10.1080/13803395.2017.1406897.

Grafman, J. (2000). Conceptualizing functional neuroplasticity. *Journal of Communication Disorders*, 33(4), 345-356. https://doi.org/10.1016/S0021-9924(00)00030-7.

Grecucci, A., Giorgetta, C., Rattin, A., Guerreschi, C., Sanfey, A. G., & Bonini, N. (2014). Time devours things: how impulsivity and time affect temporal decisions in pathological gamblers. *PLoSOne*, 9(10), e109197. https://doi.org/10.1371/journal.pone.0109197.

Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, 18(4), 196. https://doi.org/10.1038/nrn.2017.14.

Haggard, P., & Tsakiris, M. (2009). The experience of agency: Feelings, judgments, and responsibility. *Current Directions in Psychological Science*, 18(4), 242-246. https://doi.org/10.1111/j.1467-8721.2009.01644.x.

Haggard, P., Clark, S., & Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nature Neuroscience*, 5(4), 382-385. https://doi:10.1038/nn827.

Haß, K., Sinke, C., Reese, T., Roy, M., Wiswede, D., Dillo, W., Oranje, B., & Szycik, G. R. (2017). Enlarged temporal integration window in schizophrenia indicated by the double-flash illusion. *Cognitive Neuropsychiatry*, 22(2), 145-158. https://doi.org/10.1080/13546805.2017.1287693.

Hendrich, E., Strobach, T., Buss, M., Mueller, H. J., & Schubert, T. (2012). Temporal-order judgment of visual and auditory stimuli: Modulations in situations with and without stimulus discrimination. *Frontiers in Integrative Neuroscience*, 6, 63. https://doi.org/10.3389/fnint.2012.00063.

Hillock-Dunn, A., & Wallace, M. T. (2012). Developmental changes in the multisensory temporal binding window persist into adolescence. *Developmental Science*, 15(5), 688-696. https://doi.org/10.1111/j.1467-7687.2012.01171.x.

Hirst, R. J., McGovern, D. P., Setti, A., Shams, L., & Newell, F. N. (2020). What you see is what you hear: Twenty years of research using the sound-induced flash illusion. *Neuroscience & Biobehavioral Reviews*, 118, 759–774. https://doi.org/10.1016/j.neubiorev.2020.09.006.

Horr, N. K., & Di Luca, M. (2015). Filling the blanks in temporal intervals: the type of filling influences perceived duration and discrimination performance. *Frontiers in Psychology*, 6, 114. https://doi.org/10.3389/fpsyg.2015.00114.

Horr, N. K., Wimber, M., & Di Luca, M. (2016). Perceived time and temporal structure: Neural entrainment to isochronous stimulation increases duration estimates. *Neuroimage*, 132, 148-156. https://doi.org/10.1016/j.neuroimage.2016.02.011.

Hughes, G. (2018). The role of the temporoparietal junction in implicit and explicit sense of agency. *Neuropsychologia*, 113, 1-5. https://doi:10.1016/j.neuropsychologia.2018.03.020.

James, W. (1890). *The Principles of Psychology (Vol. 1)*. Holt.

Jensen, O., Kaiser, J., & Lachaux, J. P. (2007). Human gamma-frequency oscillations associated with attention and memory. *Trends in Neurosciences*, 30(7), 317-324. https://doi.org/10.1016/j.tins.2007.05.001.

Jung, R., & Berger, W. (1979). Hans bergers entdeckung des elektrenkephalogramms und seine ersten befunde 1924–1931. *Archiv für Psychiatrie und Nervenkrankheiten*, 227(4), 279-300. https://doi.org/10.1007/BF00344814.

Kawabe, T., Roseboom, W., & Nishida, S. Y. (2013). The sense of agency is action–effect causality perception based on cross-modal grouping. *Proceedings of the Royal Society B: Biological Sciences*, 280(1763), 20130991. http://dx.doi.org/10.1098/rspb.2013.0991.

Keil, J. (2020). Double flash illusions: Current findings and future directions. *Frontiers in Neuroscience*, 14, 298. https://doi.org/10.3389/fnins.2020.00298.

Keil, J., & Senkowski, D. (2017). Individual alpha frequency relates to the sound-induced flash illusion. *Multisensory Research*, 30(6), 565-578. https://doi.org/10.1163/22134808-00002572.

King, A. J. (2005). Multisensory integration: Strategies for synchronization. *Current Biology*, 15, R339–R341. https://doi.org/10.1016/j.cub.2005.04.022.

Kleiner, M., Brainard, D., Pelli, D. (2007), “What’s new in Psychtoolbox-3?” Perception 36 ECVP Abstract Supplement.

Knoblich, G., & Kircher, T. T. J. (2004). Deceiving oneself about being in control: Conscious detection of changes in visuomotor coupling. *Journal of Experimental Psychology: Human Perception and Performance*, 30(4), 657–666. https://doi.org/10.1037/0096-1523.30.4.657.

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2010). Attention and the multiple stages of multisensory integration: A review of audiovisual studies. *Acta Psychologica*, 134, 372-384. https://doi.org/10.1016/j.actpsy.2010.03.010.

Kononowicz, T. W., & van Wassenhove, V. (2016). In search of oscillatory traces of the internal clock. *Frontiers in Psychology*, 7, 224. https://doi.org/10.3389/fpsyg.2016.00224.

Konorski, J. (1948). *Conditioned reflexes and neuron organization.* Cambridge University Press.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). International affective picture system (IAPS): Technical manual and affective ratings. *NIMH Center for the Study of Emotion and Attention*, 1, 39-58.

Langille, J. J. (2019). Human REM sleep delta waves and the blurring distinction between NREM and REM sleep. *Journal of Neuroscience*, 39(27), 5244-5246. https://doi.org/10.1523/JNEUROSCI.0480-19.2019.

Lewkowicz, D. J., & Ghazanfar, A. A. (2009). The emergence of multisensory systems through perceptual narrowing. *Trends in Cognitive Sciences*, 13, 470–478. https://doi.org/10.1016/j.tics.2009.08.004.

Libet, B., Gleason, C. A., Wright, E. W., & Pearl, D. K. (1983). Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential): The unconscious initiation of a freely voluntary act. *Brain*, 106(3), 623-642. https://doi:10.1093/brain/106.3.623.

Lowel, S., & Singer, W. (1992). Selection of intrinsic horizontal connections in the visual cortex by correlated neuronal activity. *Science*, 255(5041), 209-212. DOI: 10.1126/science.1372754.

Luft, C. D. B., & Bhattacharya, J. (2015). Aroused with heart: Modulation of heartbeat evoked potential by arousal induction and its oscillatory correlates. *Scientific Reports*, 5(1), 1-11. https://doi.org/10.1038/srep15717.

Macaluso, E., George, N., Dolan, R., Spence, C., & Driver, J. (2004). Spatial and temporal factors during processing of audiovisual speech: a PET study. *Neuroimage*, 21(2), 725-732. https://doi.org/10.1016/j.neuroimage.2003.09.049.

Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers.

Proceedings of the National Academy of Sciences, 97(8), 4398-4403. https://doi.org/10.1073/pnas.070039597.

Mast, F., Frings, C., & Spence, C. (2015). Multisensory top-down sets: Evidence for contingent cross-modal capture. *Attention, Perception, and Psychophysics*, 77, 1970-1985. https://doi.org/10.3758/s13414-015-0915-4.

Matthews, W. J., Terhune, D. B., Van Rijn, H., Eagleman, D. M., Sommer, M. A., & Meck, W. H. (2014). Subjective duration as a signature of coding efficiency: emerging links among stimulus repetition, predictive coding, and cortical GABA levels. *Timing & Time Perception Reviews*, 1(1), 1-12. https://doi.org/10.1163/24054496-00101005.

McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature*, 264(5588), 746-748. https://doi.org/10.1038/264746a0.

McRaney, D. (2013). *You can beat your brain: How to turn your enemies into friends, how to make better decisions, and other ways to be less dumb*. Simon and Schuster.

Mechelli, A., Crinion, J. T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R. S., & Price, C. J. (2004). Structural plasticity in the bilingual brain. *Nature*, 431(7010), 757-757. https://doi.org/10.1038/431757a.

Metcalfe, J., Eich, T. S., & Castel, A. (2010). Metacognition of agency across the lifespan. *Cognition*, 116, 267–282. doi:10.1016/j.cognition.2010.05.009.

Metcalfe, J., & Greene, M. (2007). Metacognition of agency. *Journal of Experimental Psychology: General*, 136(2), 184-99. https://DOI:10.1037/0096-3445.136.2.184.

Metcalfe, J., Van Snellenberg, J. X., DeRosse, P., Balsam, P., & Malhotra, A. K. (2014). Judgments of agency in schizophrenia: An impairment in autonoetic metacognition. In *The cognitive neuroscience of metacognition* (pp. 367-387). Springer.

Migliorati, D., Zappasodi, F., Perrucci, M. G., Donno, B., Northoff, G., Romei, V., & Costantini, M. (2020). Individual alpha frequency predicts perceived visuotactile simultaneity. *Journal of Cognitive Neuroscience*, 32(1), 1-11. doi.org/10.1162/jocn_a_01464.

Mioni, G., Shelp, A., Stanfield-Wiswell, C. T., Gladhill, K. A., Bader, F., & Wiener, M. (2020). Modulation of individual alpha frequency with tacs shifts time perception. *Cerebral Cortex Communications*, 1(1), tgaa064. https://doi.org/10.1093/texcom/tgaa064.

Mioni, G., Stablum, F., Prunetti, E., & Grondin, S. (2016). Time perception in anxious and depressed patients: A comparison between time reproduction and time production tasks. *Journal of Affective Disorders*, 196, 154-163. https://doi.org/10.1016/j.jad.2016.02.047.

Moore, J. W., Wegner, D. M., & Haggard, P. (2009). Modulating the sense of agency with external cues. *Conscious and Cognition*, 18(4), 1056-1064. https://doi.org/10.1016/j.concog.2009.05.004.

Moore, J., & Haggard, P. (2008). Awareness of action: Inference and prediction. *Consciousness and Cognition*, 17(1), 136-144. https://doi.org/10.1016/j.concog.2006.12.004.

Moore, J.W., & Fletcher, P.C. (2012). Sense of agency in health and disease: a review of cue integration approaches. *Consciousness and Cognition*, 21, 59-68. https://doi.org/10.1016/j.concog.2011.08.010.

Mori, K. (Ed.). (2014). *The olfactory system: From odor molecules to motivational behaviors.* Springer.

Musiek, F. E., & Baran, J. A. (2018). *The auditory system: Anatomy, physiology, and clinical correlates.* Plural Publishing.

Obleser, J., & Kayser, C. (2019). Neural entrainment and attentional selection in the listening brain. *Trends in Cognitive Sciences*, 23(11), 913-926. https://doi.org/10.1016/j.tics.2019.08.004.

Ogden, R. S., Moore, D., Redfern, L., & McGlone, F. (2015). The effect of pain and the anticipation of pain on temporal perception: A role for attention and arousal. *Cognition and Emotion*, 29(5), 910-922. https://doi.org/10.1080/02699931.2014.954529.

Pacherie, E. (2013). Intentional joint agency: Shared intention lite. *Synthese*, 190(10), 1817-1839. https://doi.org/10.1007/s11229-013-0263-7.

Pearl, D., Yodashkin-Porat, D., Katz, N., Valevski, A., Aizenberg, D., Sigler, M., Weizman, A., & Kikinzon, L. (2009). Differences in audiovisual integration, as measured by McGurk phenomenon, among adult and adolescent patients with schizophrenia and age-matched healthy control groups. *Comprehensive Psychiatry*, 50(2), 186-192. https://doi.org/10.1016/j.comppsych.2008.06.004.

Plourde, M., Gamache, P.-L., & Grondin, S. (2008). Filled intervals are perceived as longer than empty ones: The effect occurs even with a between-session design. *Proceedings of Fechner Day*, 24(1), 87-93.

Powers, A. R., Hillock, A. R., & Wallace, M. T. (2009). Perceptual training narrows the temporal window of multisensory binding. *Journal of Neuroscience*, 29(39), 12265-12274. https://doi.org/10.1523/JNEUROSCI.3501-09.2009.

Rammsayer, T. H., & Lima, S. D. (1991). Duration discrimination of filled and empty auditory intervals: Cognitive and perceptual factors. *Perception & Psychophysics*, 50(6), 565-574. https://doi.org/10.3758/BF03207541.

Remington, L. A. (2011). *Clinical anatomy and physiology of the visual System* (3rd ed.). Butterworth-Heinemann.

Samaha, J., & Postle, B. R. (2015). The speed of alpha-band oscillations predicts the temporal resolution of visual perception. *Current Biology*, 25(22), 2985-2990. https://doi.org/10.1016/j.cub.2015.10.007.

Sarko, D.K., Nidiffer, A.R., Powers, A.R., Ghose, D., Hillock-Dunn, A., Fister, M.C., Krueger, J., & Wallace, M.T. (2012). Spatial and temporal features of multisensory processes: Bridging animal and human studies. In M. M. Murray & M. T. Wallace (Eds.), *The neural bases of multisensory processes.* (pp. 191-216). CRC Press/Taylor & Francis.

Sato, A. (2009). Both motor prediction and conceptual congruency between preview and action-effect contribute to explicit judgment of agency. *Cognition*, 110(1), 74-83. https://doi.org/10.1016/j.cognition.2008.10.011.

Sato, A., & Yasuda, A. (2005). Illusion of sense of self-agency: Discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition*, 94(3), 241-255. https://doi.org/10.1016/j.cognition.2004.04.003.

Schiffman, H. R., & Bobko, D. J. (1977). The role of number and familiarity of stimuli in the perception of brief temporal intervals. *The American Journal of Psychology*, 90(1), 85-93. https://doi.org/10.2307/1421643.

Schmidt, R., Ruiz, M. H., Kilavik, B. E., Lundqvist, M., Starr, P. A., & Aron, A. R. (2019). Beta oscillations in working memory, executive control of movement and thought, and sensorimotor function. *Journal of Neuroscience*, 39(42), 8231-8238. https://doi.org/10.1523/JNEUROSCI.1163-19.2019.

Shams, L., Kamitani, Y., & Shimojo, S. (2002). Visual illusion induced by sound. *Cognitive Brain Research*, 14(1), 147-152. https://doi.org/10.1016/S0926-6410(02)00069-1.

Shanks, D. R., Pearson, S. M., & Dickinson, A. (1989). Temporal contiguity and the judgement of causality by human subjects. *The Quarterly Journal of Experimental Psychology*, 41(2), 139-159. https://DOI: 10.1080/14640748908401189.

Shaw, C. A. (2001). *Toward a theory of neuroplasticity*. Psychology Press.

Shimada, S., Qi, Y., & Hiraki, K. (2010). Detection of visual feedback delay in active and passive self-body movements. *Experimental Brain Research*, 201(2), 359-364. https://doi.org/10.1007/s00221-009-2028-6.

Sidarus, N., Vuorre, M., & Haggard, P. (2017). Integrating prospective and retrospective cues to the sense of agency: A multi-study investigation. *Neuroscience of Consciousness*, 2017(1), nix012. https://doi.org/10.1093/nc/nix012.

Singh, Y., Singh, J., Sharma, R., & Talwar, A. (2015). FFT transformed quantitative EEG analysis of short term memory load. *Annals of Neurosciences*, 22(3), 176. https://doi: 10.5214/ans.0972.7531.220308.

Spence, C. (2007). Audiovisual multisensory integration. *Acoustical Science & Technology*, 28, 61-70. https://doi.org/10.1250/ast.28.61.

Spence, C. (2013). Just how important is spatial coincidence to multisensory integration? Evaluating the spatial rule. *Annals of the New York Academy of Sciences*, 1296, 31-49. https://doi.org/10.1111/nyas.12121.

Spence, C., & Squire, S. (2003). Multisensory integration: Maintaining the perception of synchrony. *Current Biology*, 13, R519–R521. https://doi.org/10.1016/S0960-9822(03)00445-7.

Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. MIT Press.

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: Current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, 9, 255-267. https://doi.org/10.1038/nrn2331.

Stevenson, R. A., & Wallace, M. T. (2013). Multisensory temporal integration: Task and stimulus dependencies. *Experimental Brain Research*, 227, 249–261. https://doi.org/10.1007/s00221-013-3507-3.

Stevenson, R. A., Altieri, N. A., Kim, S., Pisoni, D. B., & James, T. W. (2010). Neural processing of asynchronous audiovisual speech perception. *Neuroimage*, 49(4), 3308-3318. https://doi.org/10.1016/j.neuroimage.2009.12.001.

Stevenson, R. A., Segers, M., Ferber, S., Barense, M. D., & Wallace, M. T. (2014). The impact of multisensory integration deficits on speech perception in children with autism spectrum disorders. *Frontiers in Psychology*, 5, 379. https://doi.org/10.3389/fpsyg.2014.00379.

Stevenson, R. A., VanDerKlok, R. M., Pisoni, D. B., & James, T. W. (2011). Discrete neural substrates underlie complementary audiovisual speech integration processes. *Neuroimage*, 55(3), 1339-1345. doi: 10.1016/j.neuroimage.2010.12.063.

Stevenson, R. A., Wilson, M. M., Powers, A. R., & Wallace, M. T. (2013). The effects of visual training on multisensory temporal processing. *Experimental Brain Research*, 225(4), 479-489. https://doi.org/10.1007/s00221-012-3387-y.

Swart, T., Chisholm, K., & Brown, P. (2015). *Neuroscience for leadership: Harnessing the brain gain advantage.* Springer.

Synofzik, M., Vosgerau, G., & Newen, A. (2008). Beyond the comparator model: A multifactorial two-step account of agency. *Consciousness and Cognition*, 17(1), 219-239. https://doi.org/10.1016/j.concog.2007.03.010.

Synofzik, M., Vosgerau, G., & Voss, M. (2013). The experience of agency: an interplay between prediction and postdiction. *Frontiers in Psychology*, 4, 127. https://doi.org/10.3389/fpsyg.2013.00127.

Terhune, D. B., & Hedman, L. R. (2017). Metacognition of agency is reduced in high hypnotic suggestibility. *Cognition*, 168, 176-181. https://doi.org/10.1016/j.cognition.2017.06.026.

Thaler, L., Arnott, S. R., & Goodale, M. A. (2010). Human echolocation I. *Journal of Vision*, 10(7), 1050-1050. https://doi.org/10.1167/10.7.1050.

Thomas, E. C., & Brown, I. (1974). Time perception and the filled-duration illusion. *Perception & Psychophysics*, 16(3), 449-458. https://doi.org/10.3758/BF03198571.

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the" internal clock". *Psychological Monographs: General and Applied*, 77(13), 1. https://doi.org/10.1037/h0093864.

Treisman, M. (2013). The information-processing model of timing (Treisman, 1963): Its sources and further development. *Timing & Time Perception*, 1(2), 131-158. https://doi.org/10.1163/22134468-00002017.

Treisman, M., Cook, N., Naish, P. L., & MacCrone, J. K. (1994). The internal clock: electroencephalographic evidence for oscillatory processes underlying time perception. *The Quarterly Journal of Experimental Psychology Section A*, 47(2), 241-289. https://doi.org/10.1080/14640749408401112.

Treisman, M., Faulkner, A., Naish, P. L., & Brogan, D. (1990). The internal clock: Evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception*, 19(6), 705-742. https://doi.org/10.1068/p190705.

Van der Burg, E., Olivers, C. N. L., Bronkhorst, A. W., & Theeuwes, J. (2008). Non-spatial auditory signals improve spatial visual search. *Journal of Experimental Psychology: Human Perception and Performance,* 34, 1053-1065. https://doi.org/10.1037/0096-1523.34.5.1053.

Van Eijk, R. L., Kohlrausch, A., Juola, J. F., & Van de Par, S. (2008). Audiovisual synchrony and temporal order judgments: Effects of experimental method and stimulus type. *Perception & Psychophysics,* 70(6), 955-968. https://doi.org/10.3758/PP.70.6.955.

Van Rullen, R. (2016). Perceptual cycles. *Trends in Cognitive Sciences,* 20(10), 723-735. https://doi.org/10.1016/j.tics.2016.07.006.

Van Wassenhove, V., Grant, K. W., & Poeppel, D. (2007). Temporal window of integration in auditory-visual speech perception. *Neuropsychologia*, 45, 598–607. https://doi.org/10.1016/j.neuropsychologia.2006.01.001.

Vatakis, A. (2013). *The role of stimulus properties and cognitive processes in the quality of the multisensory perception of synchrony.* In L. Albertazzi (Ed.), Handbook of experimental phenomenology: Visual perception of shape, space and appearance (pp. 243–263). John Wiley and Sons.

Venskus, A., Ferri, F., Migliorati, D., Spadone, S., Costantini, M., & Hughes, G. (2021). Temporal binding window and sense of agency are related processes modifiable via occipital tACS. PlosOne, https://doi.org/10.1371/journal.pone.0256987.

Venskus, A., & Hughes, G. (2021). Individual differences in alpha frequency are associated with the time window of multisensory integration, but not time perception. *Neuropsychologia,* 107919. DOI: 10.1016/j.neuropsychologia.2021.107919.

Vosgerau, G., & Synofzik, M. (2012). Weighting models and weighting factors. *Consciousness and Cognition*, 21(1), 55-58. https://doi.org/10.1016/j.concog.2011.09.016.

Vroomen, J., & Keetels, M. (2010). Perception of intersensory synchrony: A tutorial review. *Attention, Perception, & Psychophysics*, 72, 871–884. https://doi.org/10.3758/APP.72.4.871.

Wang, W., Datta, H., & Sussman, E. (2005). The development of the length of the temporal window of integration for rapidly presented auditory information as indexed by MMN. *Clinical Neurophysiology*, 116(7), 1695-1706. https://doi.org/10.1016/j.clinph.2005.03.008.

Watson, A. B. (1986). Temporal sensitivity. *Handbook of Perception and Human Performance*, 1(6), 1-43. https://doi:10.1136/bmjspcare-2011-000020.16.

Wearden, J. H., & Penton-Voak, I. S. (1995). Feeling the heat: Body temperature and the rate of subjective time, revisited. *The Quarterly Journal of Experimental Psychology Section B*, 48(2b), 129-141. https://doi.org/10.1080/14640749508401443.

Wearden, J. H., Norton, R., Martin, S., & Montford-Bebb, O. (2007). Internal clock processes and the filled-duration illusion. *Journal of Experimental Psychology: Human Perception and Performance*, 33(3), 716. https://doi.org/10.1037/0096-1523.33.3.716.

Wearden, J. H., O'Rourke, S. C., Matchwick, C., Min, Z., & Maeers, S. (2010). Task switching and subjective duration. *Quarterly Journal of Experimental Psychology*, 63(3), 531-543. https://doi.org/10.1080/17470210903024768.

Wegner, D. (2002). *The Illusion of Conscious Will.* Cambridge, MA: MIT Press.

Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, 88(3), 638. https://doi.org/10.1037/0033-2909.88.3.638.

Wenke, D., Fleming, S. M., & Haggard, P. (2010). Subliminal priming of actions influences sense of control over effects of action. *Cognition*, 115(1), 26-38. https://doi:10.1016/j.cognition.2009.10.016.

White, T. P., Wigton, R. L., Joyce, D. W., Bobin, T., Ferragamo, C., Wasim, N., Lisk, S., & Shergill, S. S. (2014). Eluding the illusion? Schizophrenia, dopamine and the McGurk effect. *Frontiers in Human Neuroscience*, 8(565), 1-12. https://doi.org/10.3389/fnhum.2014.00565.

Williams, E. A., Yüksel, E. M., Stewart, A. J., & Jones, L. A. (2019). Modality differences in timing and the filled-duration illusion: Testing the pacemaker rate explanation. *Attention, Perception, & Psychophysics*, 81(3), 823-845. https://doi.org/10.3758/s13414-018-1630-8.

Wittmann, M., and van Wassenhove, V. (2009). The experience of time: neural mechanisms and the interplay of emotion, cognition and embodiment. *Philosophical Transactions: Biological Sciences*, 364, 1809–1813. https://doi.org/10.1098/rstb.2009.0025.

Wittmann, M., Simmons, A. N., Aron, J. L., & Paulus, M. P. (2010). Accumulation of neural activity in the posterior insula encodes the passage of time. *Neuropsychologia*, 48(10), 3110-3120. https://doi.org/10.1016/j.neuropsychologia.2010.06.023.

Yoo, J. Y., & Lee, J. H. (2015). The effects of valence and arousal on time perception in individuals with social anxiety. *Frontiers in Psychology*, 6, 1208. https://doi.org/10.3389/fpsyg.2015.01208.

Zakay, D., & Block, R. A. (1996). The role of attention in time estimation processes. *Advances in Psychology*, 115, 143-164. https://doi.org/10.1016/S0166-4115(96)80057-4.

Zampini, M., Guest, S., Shore, D. I., & Spence, C. (2005). Audio-visual simultaneity judgments. *Perception & Psychophysics*, 67(3), 531-544. https://doi.org/10.3758/BF03193329.

Zerr, M., Freihorst, C., Schütz, H., Sinke, C., Müller, A., Bleich, S., Münte, T. F., & Szycik, G. R. (2019). Brief sensory training narrows the temporal binding window and enhances long-term multimodal speech perception. *Frontiers in Psychology*, 10, 2489. https://doi.org/10.3389/fpsyg.2019.02489.

Zhang, Y., Zhang, Y., Cai, P., Luo, H., & Fang, F. (2019). The causal role of α-oscillations in feature binding. *Proceedings of the National Academy of Sciences*, 116(34), 17023-17028. https://doi.org/10.1073/pnas.1904160116.

Zhou, Y. J., Iemi, L., Schoffelen, J. M., de Lange, F. P., & Haegens, S. (2021). Alpha oscillations shape sensory representation and perceptual accuracy. *bioRxiv*. https://doi.org/10.1101/2021.02.02.429418.

Zmigrod, S., & Hommel, B. (2011). The relationship between feature binding and consciousness: Evidence from asynchronous multi-modal stimuli. *Consciousness and Cognition*, 20(3), 586-593. https://doi.org/10.1016/j.concog.2011.01.011.